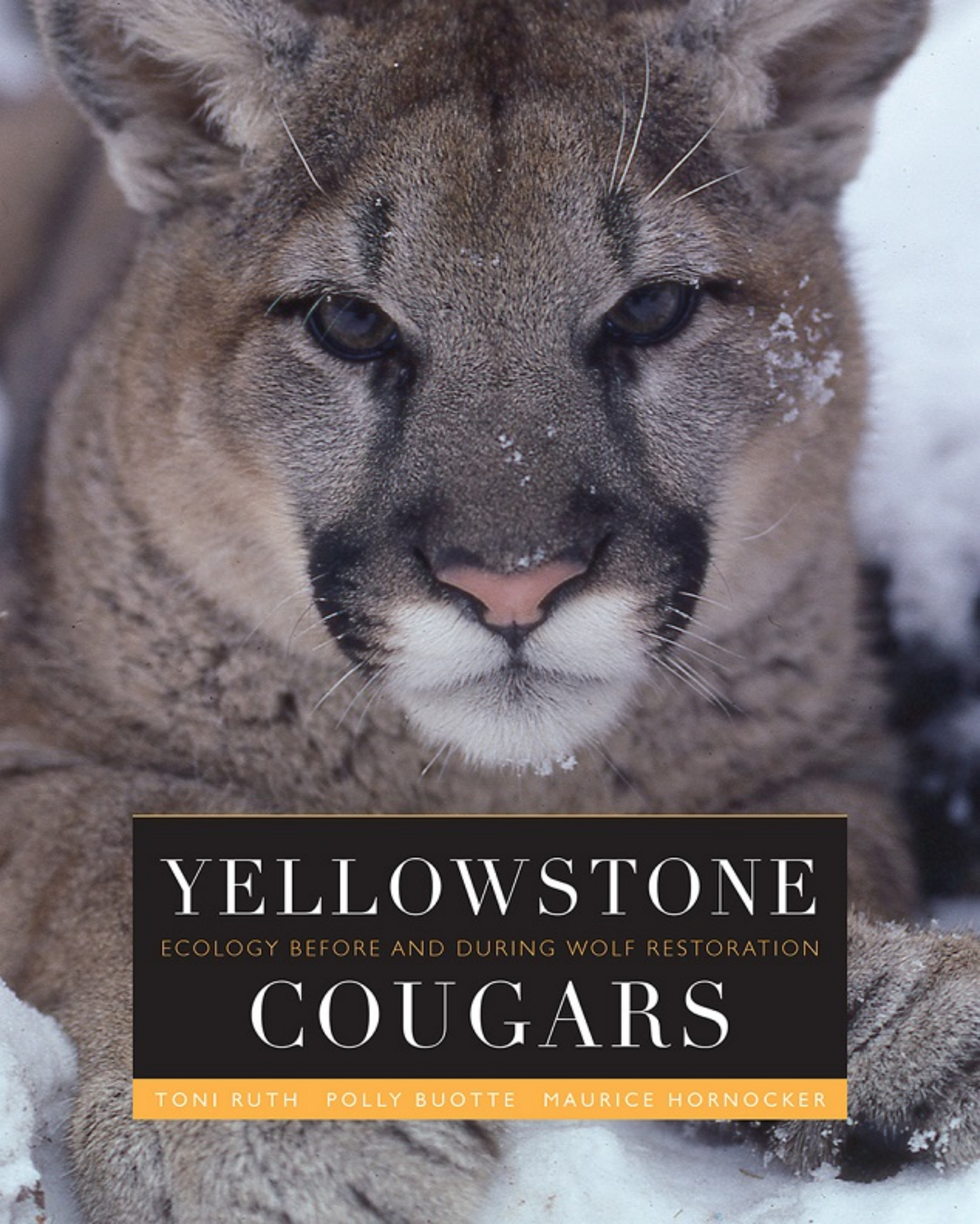




# YELLOWSTONE

ECOLOGY BEFORE AND DURING WOLF RESTORATION

# COUGARS

TONI RUTH POLLY BUOTTE MAURICE HORNOCKER

VISIT...

LANZAROTE  
*Caliente*.COM

# Yellowstone Cougars





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ECOLOGY BEFORE AND DURING WOLF RESTORATION

Toni K. Ruth, Polly C. Buotte, and Maurice G. Hornocker

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## Foreword

L. DAVID MECH

*Senior Research Scientist, USGS Adjunct Professor,  
University of Minnesota*

Cougars were not much on our minds when Maurice Hornocker and I sat down in Yellowstone National Park with Nathaniel Reed, Assistant Secretary of the Interior during the Nixon administration. That meeting was over 40 years ago, and Reed had invited us to plot reintroducing wolves to the park. The big cat was already there, though sparsely, but there wasn't a wolf within 400 miles (640 km). Nat was keen on getting them there and thought both Maurice and I, and bear biologist Chuck Jonkel, could help him plan a strategy. The only wolves left in the 48 contiguous US were in Minnesota and Isle Royale National Park in Lake Superior. They had been listed as endangered in 1967 and federally protected by the Endangered Species Act of 1973.

Fast forward to March 23, 2001, and to Hellroaring Lookout, one of Yellowstone's most scenic overlooks. There, no doubt, Nat, Maurice, Chuck, and I had, decades before, speculated about what it would be like to observe wolves from there. On this day a quarter-century later, I was standing there again with a group from the International Wolf Center, including then executive director, Walter Medwid, actively watching for wolves that had just left an elk kill they had made. Walter kept his scope on the kill, observing the ravens and a golden eagle scavenging the remains way below in a clearing.

All of a sudden, we heard Walter exclaim, "Oh, my god; oh, my god; oh my god; it's a cougar!" Extended tail trailing behind, a tawny, lanky mountain lion was bounding into the scene, chasing the eagle away from the kill. Switching my scope from scanning for wolves to focusing on the kill, I celebrated my first-ever view of the wolves' big feline competitor. What a sight it was!

The cougar was wearing one of Toni Ruth's radio collars that thus allowed her to monitor the animal's movements

and activity. I'm sure the data found its way into this unique book about Yellowstone's lions' interactions with the wolves that Nat Reed and so many of us so long ago wanted restored to the park.

Along with a team of about 30, I helped collect the wolves from Canada that we reintroduced into Yellowstone in 1995 and 1996. Each year since then I've spent time there studying them. Thus, while Toni and her colleagues Maurice Hornocker and Kerry Murphy studied cougars in the park, my grad students, Yellowstone colleagues, and I researched the wolves and their prey. Although we wolf and lion biologists rarely ran into each other, our study animals often did. Even when they didn't, their predation and basic behavior affected each other: two top predators both dependent on Yellowstone's several hoofed species. This book's chapter titles portray the many details of those very interesting interactions. A sampling: "Prey Selection by Cougars and Wolves," "Direct Interactions at Kills," "Synthesis: The Niches of Cougars and Wolves," "How Might Cougars Respond to Wolves?"

As one who has always wondered about these subjects, I am grateful that these authors, including Kerry Murphy and Doug Smith on some of the chapters, have assembled all this information in one place, and I commend them for it. The results call to mind the only other times I have seen lions in the park, once from a helicopter and once from a bridge.

While Shannon Barber-Meyer and I were flying around searching for newborn elk calves to radio-collar for her PhD work, I once looked down and spotted three of the big cats. Although the chopper pilot was skeptical of my report of this unusual sighting of three adult-sized cougars, he whirled the craft around, and we took a good look. Sure enough, three lithe lions leaped up and bounded away,



almost certainly a mother and two grown kittens. I'm sure Toni would know because at least one of them wore a radio collar.

The last time I watched a lion in the park was 2016, this one not collared. She was feeding on an elk kill and was putting on quite a show for a crowd on the bridge just south of Mammoth. Having spent almost 60 years observing wolves, including many in Yellowstone, getting this rare

chance to watch a cougar for only the third time was a far greater treat.

And a real treat it is to see this wonderful book materialize. It will give many thousands of readers an opportunity not only to see intimately into the lives of both the majestic cat and the grand canid that stalk Yellowstone National Park, but also into the interesting interactions of these competing carnivores.

## Acknowledgments

The investigation of cougars, wolves, and their competition for prey and space in the Greater Yellowstone Ecosystem and Greater Yellowstone Northern Range was fascinating, challenging, and filled with surprises. Following cats day in and day out revealed special hidden places in Yellowstone. This important work would not have transpired without the generous logistical and funding support and collaboration of many people, foundations, organizations, and colleagues. We thank them for making it possible.

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Service, and Yellowstone National Park. Thank you for your commitment to understanding our natural world.

Alongside Maurice, Howard Quigley was instrumental in initiating the second phase of cougar research during wolf restoration in Yellowstone and has been key to its continued success. During Howard's tenure as president of the Hornocker Wildlife Institute, his keen interest in understanding the ecology and interactions of all large carnivores residing on the Northern Range buoyed our efforts by melding our collaboration with the Yellowstone Wolf Project and the Interagency Grizzly Bear Study Team into the Large Carnivore Working Group.

We are deeply indebted to personnel at a suite of agencies and universities for helping us navigate paperwork, facilitating our safety while in the field, and providing advice and logistical and in-kind support throughout our studies: Yellowstone National Park; Montana Department of Fish, Wildlife and Parks; US Forest Service Gallatin National Forest, USGS Interagency Grizzly Bear Study Team, University of Idaho, Montana State University, Wyoming Game and Fish, and the US Fish and Wildlife Service.

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fed, cuddled, festooned with hats, and laughing. My good friend Rob Jensen opened his home to me during my long stay in Missoula. I can never repay him for his generosity.

I am profoundly thankful for the journey I have taken with Maurice and Polly. Maurice provided me with an amazing opportunity to study cougars in the Greater Yellowstone Ecosystem. He afforded me the independence to develop my research ideas without the worry of how to keep the project afloat financially. I am forever grateful. After her arrival, Polly became such an essential part of the project that I cannot imagine completing it without her. The opportunity to work and become friends with Maurice and Polly, their integrity and dedication to wildlife science, and their warm hearts have inspired me in so many ways. I will cherish their friendship and shared memories for the rest of my days.

—TONI RUTH

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It is nearly impossible for me to convey the gratitude I feel for having been a part of this work. I wholeheartedly thank Maurice, Toni, and Howard for that opportunity. Their combined vision shaped a remarkable research project that was conducted with integrity and compassion. From fieldwork to data analysis and writing to off the clock, Toni has been a remarkable supervisor and role model and a true friend. I am also grateful to Mike Maples, Jesse Newby, Mike Sawaya, and Dan Stahler for our time in and out of the field—I have never had better field partners.

—POLLY BUOTTE

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I can only echo Toni Ruth's thanks to all those individuals, organizations, and entities who contributed to this overall effort. Without their help the project would not have been successful.

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This book stands as a tribute to Toni Ruth. Her professionalism and scientific integrity are admired by all who know her. But without her passion, dedication, and personal courage this book would not be a reality. Her efforts are simply unmatched in my experience.

Polly Buote completed the team. She and Toni shared all aspects of the research, forging amazingly successful cross-agency cooperation. For long-term research this is absolutely essential.

Finally, I wish to dedicate my contribution to this work to my mentors, John Craighead and Wilbur Wiles. John taught

me there is no greater joy than that of discovery, especially something new. Wilbur observed, “The more we learn the more we learn we don’t know.” I think they both would approve of this book.

—MAURICE HORNOCKER

# Yellowstone Cougars





## **PART I**

### **Cougar Studies before and during Wolf Restoration**

Competition is one of the most important factors controlling the distribution and abundance of living creatures. There are beetles that compete in arenas for access to dung balls, tadpoles that apparently poison their neighbors, birds that smash the eggs of potential competitors.

PAUL KEDDY, *COMPETITION* (2ND EDITION, 2001)





## CHAPTER I

### Introduction and Background

What carnivores eat, their hunting behavior and habitat use, and how they survive is not only a function of their predatory nature but also hinges on the pivotal role other large carnivores play in the lives of less dominant ones—by competing with them for food, by preying on them, or both (Creel 1998; Ballard et al. 2003; Caro and Stoner 2003). In some instances, competition for resources determines whether one predator is even allowed to live where another predator exists, which can have important implications for carnivore management and conservation (Donadio and Buskirk 2006; Murphy and Ruth 2010). For instance, rare African wild dogs do not fare well where African lion and spotted hyena densities are high (Creel and Creel 1996, 2002). Competition with coyotes (*Canis latrans*) reduces survival of endangered San Joaquin kit foxes (*Vulpes macrotis multica*), although kit foxes reduce some of this predation mortality by avoiding coyote-dominated shrub habitats (Cypher and Spencer 1998; Nelson et al. 2007). Hence, along with predation, competition between carnivores for resources has important implications for the structure and function, as well as conservation, of ecological communities (Schoener 1982; Palomares and Caro 1999; Linnell and Strand 2000; Creel et al. 2001; Caro and Stoner 2003).

At the time of European settlement of North America, cougars (*Puma concolor*), wolves (*Canis lupus*), black bears (*Ursus americanus*), and brown bears (*U. arctos*) were widely distributed, occupying diverse habitats (Wilson and Ruff 1999; Laliberte and Ripple 2004). Such extensive distribution meant that many carnivores were regionally sympatric, and during their co-evolution, interspecific interactions and competition may have been one of several evolutionary forces contributing to the structure of assemblages of carnivores in the various environments (Schaller 1972; Mills 1990;

Caro 1994; Durant 1998). As human settlement increased, particularly in the 1800s and early 1900s, people altered habitats and drastically changed carnivore distribution and abundance. In most of the United States, the complex system of interactions between these species was altered or eliminated. Large carnivores now occupy remnants of their former distribution—grizzly bears persist in roughly 45 percent of their historical range and cougars and wolves in about 60 percent of theirs (Laliberte and Ripple 2004: 126).

Although scientific research has advanced our understanding of carnivores substantially since the early 1970s, we are still learning how to live with cougars and wolves and how best to understand their management and conservation needs in the various states where they remain or are becoming restored (Mech and Boitani 2003a; Hornocker and Negri 2009; Jenks 2011). During the time we were writing this book, wolves in Idaho and Montana reached numbers that met federal goals for recovery from endangered status; they were frequently in the news, and their status was haggled over in and out of the courts. Wolves were delisted from endangered status in 2008, quickly relisted after litigation, and delisted again in 2009. They were hunted in Idaho and Montana in the winter of 2009–10, relisted as endangered in August 2010, and then fully delisted, with hunting resumed in both states in late 2011 (Idaho Department of Fish and Game 2012). Later, on September 30, 2012, Wyoming assumed management authority for wolves (Wyoming Game and Fish Department 2013). Meanwhile, cougars were in the news as they worked their way eastward, showing up on remote cameras, shot in farmers' fields, or killed along highways in Nebraska, Missouri, Michigan, Wisconsin, and other mid-western states (Cougar Network 2012).

Questions concerning how species within the large carnivore guild interact, how they partition resources, and what enables or hampers their coexistence are pertinent to management and conservation of these large species as they are restored in our human-dominated landscape. However, in most ecosystems in North America, little information has accumulated regarding such interspecific interactions. This is the case for several reasons. Sustaining long-term ecological studies of large carnivore populations is challenging and expensive because they necessitate working at large spatial scales (Hobbs 1996; Garrott and White 2009). In addition, the rarity of multi-species carnivore assemblages has made investigation of communities of carnivores less common than the single-species approaches that have thus predominated in conservation efforts for these large species. Hence it is not surprising that much of what we have learned about cougars has occurred in the absence of wolves, their main natural competitors.

Given limited funding and logistical support, many studies on cougars have lasted only two to four years—far short of the cougar's natural life span of twelve to fourteen years for females in the wild. However, more recently, a number of studies have provided continual investigation over eight years or more (Beier 1996; Logan and Sweanor 2001; Maehr et al. 2002; Beier et al. 2003; Laundré and Clark 2003; Laundré et al. 2007). In comparison, much greater numbers of short- and long-term research studies have amassed critical information on wolves and bears, both in and beyond Yellowstone National Park. But again, most of these studies, including the famous studies of wolves in Alaska and Michigan (see Mech 1970; Carbyn et al. 1995; Mech and Boitani 2003a), have occurred in the absence of cougars.

Today only a few relatively intact ecosystems remain where we can further our understanding of interactions among multiple large carnivores. With the restoration of wolves in 1995 and 1996, the Greater Yellowstone Ecosystem became one of these.

This book is about cougar ecology and how cougars responded to the restoration of their main competitors, wolves, on the Greater Yellowstone Northern Range. At its core, our research was directed toward understanding whether cougars and wolves would compete for certain resources directly and indirectly, how they might sort out the landscape as a result of competition and avoidance, and whether wolves negatively affected cougar population

performance, including survival and reproduction. These questions encompass topics that have been of interest to the general public, hunters, agencies charged with management of these controversial top carnivores, and conservationists seeking to incorporate ecological and community information into long-term wildlife conservation.

The book is arranged in five parts consisting of eighteen chapters. This first part covers background on development of the project and includes the evolutionary history and taxonomy of cougars and wolves, describes the study area, highlights how we went about quantifying competition and coexistence, and describes our methods of studying cougars before and during wolf restoration. Prey selection, kill rates, and interactions at kills are the focus of part 2. Part 3 addresses whether the movement behavior and spatial-habitat use patterns of cougars changed after wolf restoration. In part 4 we assess whether reproduction, survival, and numbers of cougars have been negatively influenced by the presence of wolves. Finally, in part 5 we synthesize our findings and present our ideas for the management and conservation of cougars in the Greater Yellowstone Ecosystem and in states where cougars and wolves are now naturally being restored.

## **CO-EVOLUTION AND TAXONOMY OF COUGARS AND WOLVES**

Up until the time they were eradicated by humans from much of their range, cougars and wolves shared a long evolutionary history across North, Central, and South America. At one time cougars had the broadest geographic distribution of any terrestrial mammal in the Western Hemisphere (Logan and Sweanor 2001; Cougar Management Guidelines Working Group 2005; Culver 2010).

Cougars, wolves, and other extinct and extant carnivores originated from a common ancestor between 65 million and 55 million years ago during the Miocene—from a tree-dwelling shrew-like predator called a miacid that scurried after insects (Ewer 1973; Macdonald 1992). At the base of the carnivores' story were two types of miacids, one that probably looked much like modern martens—vulpavines—and the other resembling modern genets—viverravines. These early arboreal carnivores gave rise to two main branches of the order Carnivora: the Canoidea arose from the vulpavines of the New World, and the Feloidea arose from the Old World viverravines (Ewer 1973; Kleiman and Eisenberg 1973; Macdonald 1992).

The teeth of the Canoidea and Feloidea exemplify the differences in skeletal structure that separate these two major divisions. In the canids, one of the lower carnassials retains a broad shelf (taloid) that provides a dual function—cutting at the front and crushing behind—which enables mastication of food; hence, digestion can begin in the mouth (Tedford 1994). As a result, dogs and their close relatives can process a variety of foods—meat, bone, sinew, invertebrates, plants—which provides great survival value because the wider range of food enables the canids to adapt to shifting resources as local conditions dictate. The dog branch diversified and gave rise to four caniform families: dogs (Canidae), bears (Ursidae), weasels (Mustelidae), and raccoons (Procyonidae). Members of the cat group, in contrast, lack the taloid shelf, and their molars are all specialized to cut meat and deliver the chunks whole to the stomach for digestion (Tedford 1994). Four feliform families sprouted from the cat branch: cats (Felidae), civets (Viverridae), hyenas (Hyaenidae), and mongooses (Herpestidae).

Tracing the diversification of modern felids and canids is not easy (Ewer 1973; O'Brien and Johnson 2007). Fortunately, advances in DNA sequencing have allowed mapping of the genomes of various species, which made it possible to construct the first resolved family tree for cats (Culver 1999; O'Brien and Johnson 2007) and an improved tree for the dog family (Wayne and Vilà 2003).

### Evolutionary History of Cougars and Wolves

Before modern carnivore families appeared, the dog and cat branches evolved separately in the New World and the Old World. When the Bering land bridge opened up between America and Eurasia roughly 30 million years ago, representatives of each branch made the crossing, and dogs and cats came face to face (Macdonald 1992).

The cougar belongs to the extremely old puma lineage, members of which originated from a common North American ancestor roughly 7 million to 8 million years ago (Culver 2010). The puma lineage also includes the cheetah (*Acinonyx jubatus*) and jaguarondi (*Puma yaguarondi*), with the cheetah first to diverge from the common felid ancestor about 5 million to 8 million years ago, making it the second closest relative of the cougar (Johnson and O'Brien 1997; Turner and Antón 1997; Culver 2010). Later, the jaguarondi and cougar diverged around 4 million to 5 million years

ago, making them the closest relatives in the puma lineage (Janczewski et al. 1995; Johnson and O'Brien 1997; Johnson et al. 2006; Culver 2010).

Fossil evidence in North America suggests that cougars or an ancestor may have evolved in North America and migrated to southern continents approximately 2 million to 4 million years ago (Patterson and Pascual 1968; Webb 1976; Logan and Sweanor 2001; Culver 2010). But more recent research using genetic tools finds disagreement between the fossil record and the molecular data. Specifically, molecular analyses indicate that the oldest cougar population inhabits Brazil and Paraguay, the North American population is the most recently founded, and cougars as a species are ~0.39 million years old (Culver et al. 2000). Around 10,000–17,000 years ago, during the late Pleistocene, the North American cougar population experienced a demographic contraction event, or “bottleneck,” persisting as a small population while many other large mammals went extinct (Driscoll et al. 2002). Descending from a “founder event” involving this small number of individuals, modern North American cougars then expanded from the south, where populations remained stable, to the north, where populations had been extirpated (Culver et al. 2000; Culver 2010). This relatively young age for cougars in North America is directly related to the lack of genetic diversity and differentiation observed in extant North American cougars (Culver 2010: 33). Providing further evidence to support expansion from south to north, molecular genetic data show higher levels of genetic variation among cougars in California and Arizona–New Mexico than among cougars residing farther north (Ernest et al. 2003; McRae et al. 2005).

Wolves arose at about the same time cougars did. By the Pliocene, *Canis* had diversified and become widespread in both the Old World and North America, with wolf-like canids diverging from a common ancestor approximately 2 million to 3 million years ago (Nowak 1979; Wayne et al. 1995). A related branch of small canids entered South America and began an entirely separate evolutionary lineage (Nowak 1979; Kurtén and Anderson 1980; Tedford et al. 1995). It is likely that wolves arose from some population of those small early canids and that the ancestral line also led to coyotes (Nowak 2003). Wolf and coyote lineages diverged between 2.5 million and 1.8 million years ago, not long after divergence of the cougar and jaguarondi lineages (Kurtén 1974; Nowak 1979).

The emergence of modern wolves occurred sometime between 300,000 and 130,000 years ago (Nowak 1979; Wayne et al. 1995). An ancestor to today's wolves probably arose in North America and crossed via the Bering land bridge into Eurasia, where it evolved in the direction of *C. lupus*, the gray wolf (Nowak 2003). The gray wolf is thought to have developed fully in the Old World and then reinvaded the New World in the Pleistocene by once again crossing the Bering land bridge (Nowak 1979; Kurten and Anderson 1980; Brewster and Fritts 1995). Wolf populations of the Old and New World show varying degrees of genetic subdivision, and this, in combination with the extremely high mobility of wolves, suggests the effect of multiple invasions following the numerous glacial advances and retreats of the Pleistocene (Wayne et al. 1992; Forbes and Boyd 1996, 1997; Vilà et al. 1999a).

Regardless of their exact point of origin, cougars and wolves fared well after the late Pleistocene extinctions when the demise of mega-herbivores led to the demise of many of the larger carnivores (Macdonald 1992). Five species of carnivorous mammals disappeared from North America at the end of the Pleistocene: giant short-faced bear, American lion, American cheetah, sabertooth, and dire wolf (Pielou 1991). As many of the larger carnivores went extinct, interspecific competition would have declined somewhat, and the midsized cougar was well adapted to subsist on the smaller, soft-skinned grazers as well as on a wide range of other prey in various habitats (Logan and Sweanor 2001). After the extinction of their dominant competitor, the dire wolf (*C. dirus*), about 8,000 years ago, gray wolf populations grew and remained abundant until they were all but exterminated by modern hunters (Pielou 1991). Along with cougars and wolves, several other midsized to large North American carnivores survived the extinctions: grizzly and black bears, wolverines, coyotes, badgers, red and gray foxes, lynxes and bobcats, and polar bears (Pielou 1991). Thus, in addition to wolves, cougars still had to contend with a few formidable competitors.

### Taxonomy

From the mid-1700s to the mid-900s—using morphological characteristics, habitat, and general geographic distribution—biologists described thirty-two distinct subspecies of the cougar, distributed throughout North and South America (Young and Goldman 1946). The cougar was orig-

inally named *Felis concolor* by Linneaus in 1771 (Wozencraft 1993; Culver 2010) and later renamed *Felis (Puma) concolor* when Jardine (1834) recognized *Puma* as a subgenus of *Felis*. Although *Puma* was recognized as a separate genus as recently as 1973 (Ewer 1973), *Felis* remained the more commonly referenced genus until the mid-1990s. By then, taxonomy could draw upon molecular genetics to examine the accuracy of generic and subspecific divisions. When cougar DNA was analyzed from blood and tissue samples collected throughout the Americas, Culver and colleagues (2000) determined that there were six groups of cougars, not thirty-two, across their range. One cougar subdivision occurred from Nicaragua northward and five subdivisions existed south of Nicaragua. Apparently, cougars had been breeding with each other, wandering great distances to do so and even swimming substantial bodies of water, over much larger areas than originally thought. In South America a high level of genetic diversity was found in cougars, whereas Central and North American cougars, north of Nicaragua, had only moderate levels (microsatellite DNA) to no variation (mitochondrial DNA). Culver and co-workers (2000, 2011) eventually proposed taxonomic revisions to include the six subspecies: in North America *Puma concolor cougar*, Central America *P. c. costaricensis*, northern South America *P. c. concolor*, eastern South America *P. c. capricornensis*, central South America *P. c. cabreræ*, and southern South America *P. c. puma*.

Worldwide, the gray wolf has also been divided into as many as thirty-two subspecies (Hall and Kelson 1959; Wayne and Vilà 2003). But in contrast to the situation for cougars, the rates of gene flow and geographic variation among North American wolf populations are high. Rather than populations partitioned into discrete geographic areas, geographic variation in the wolf is distributed along a continuum (Nowak 2003; Wayne and Vilà 2003). Thus the division of wolves into discrete subspecies and other genetic units may be somewhat arbitrary (Wayne and Vilà 2003), although Forbes and Boyd (1996) found a limited pattern of genetic differentiation with increasing geographic distance. Now biologists consider the gray wolf part of a single monophyletic clade (Wayne et al. 1995; Wayne and Vilà 2003). In fact, all species in the genus *Canis*, as well as the dhole and the African hunting dog, possess identical numbers of chromosomes (Wayne et al. 1978a, 1978b; Wurster-Hill and Centerwall 1982).



## Hounds from Wolves: The Path to Hunting Cougars

The extant species most closely related to the gray wolf is the domestic dog (*C. l. familiaris*; Tsuda et al. 1997; Vilà et al. 1997, 1999a; Leonard et al. 2002; Savolainen et al. 2002). Using mitochondrial DNA, Savolainen and colleagues (2002) concluded that domestic dogs had a single origin about 15,000 years ago in East Asia. Early wolf-dogs probably associated with humans primarily for food, and imprinting on humans from an early age would have facilitated the domestication process (Mech 1970; Olsen 1985). The dogs of the Western Hemisphere derive from the domesticated descendants of these Old World wolves that trekked with humans over the Bering land bridge (Leonard et al. 2002). Some of these early dogs also accompanied humans to western Asia and Europe, where they played a role in founding some of today's breeds (Leonard et al. 2002; Kerasote 2007).

Most hound breeds are descendents of the bloodhound, the most ancient breed of hound. Thought to have originated in France or England, bloodhounds have been put to work for hundreds of years tracking humans and other animals. Historical accounts of bloodhounds provide little evidence for how far back the origins of the breed reach, but many authorities believe the breed was known throughout the Mediterranean countries long before the Christian era (Brough 2007). Although no evidence exists, some claims indicate that the bloodhound ancestors referenced in English writing in the mid-fourteenth century were brought over from Normandy by William the Conqueror after the conquest of 1066 (Barwick 2006; Bloodhounds UK 2011). Scottish and English records from the fourteenth century also suggest that the rebel William Wallace (popularized in Mel Gibson's film *Braveheart*) was tracked by sleuth hounds, which many believe to be the same as the bloodhound. What is clear is that by the mid-fourteenth century, the English had a large, keen-scented hound that, similar to wolves, was adept at tracking, pursuing, and keeping at bay raccoons, bears, and cougars and other felid species.

The danger-avoidance behavior known as treeing—a trait that is common to cougars, bobcats, and black bears—evolved solely for the purpose of reducing interference competition with pack-living wolves and other dominant carnivores, including grizzly bears (Herrero 1978). The persistence of this instinctive behavior, even in areas where for over a century cougars did not need to avoid competition from wolves,



**FIGURE 1.1.** Buck (left) and Cooter doing their job during the capture of adult female F125. Photo by Tony Knuchel, Hornocker Wildlife Institute.

exemplifies the “ghost of competition past” (Connell 1980). Although wolves did not operate as the selective force for this trait for fifty to sixty years, pursuit of cougars by hunting hounds in many states has perhaps helped maintain selective pressure for treeing as an advantageous survival trait. Thus, houndsmen who enjoy watching their dogs trail a cougar or bobcat, and researchers who use hounds to capture and mark cougars for study purposes, can link the hounds’ fine tracking abilities to their ancestor, the wolf (fig. 1.1).

## DEVELOPMENT OF OUR FOURTEEN-YEAR RESEARCH STUDY

A growing public desire to prevent the loss of threatened wildlife finds expression today in legislation as well as calls for federal and state agencies to form management and conservation strategies that incorporate the latest and best scientific information (e.g., Florida panther and black bear, Alvarez 1993). However, with the exception of game species, endangered species, or those with greatest conservation need, federal and state resource agencies typically are not funded or structured to conduct the intensive long-term biological research necessary to further the management-conservation process for large carnivores. Nonprofit conservation organizations have frequently played a success-

ful role in filling this gap, and one such nonprofit was the impetus behind the fourteen-year study resulting in this book.

Guided by founder and director Dr. Maurice Hornocker, the Hornocker Wildlife Institute was a small, effective organization with a record of providing new information to agencies and the public by investing in long-term scientific studies. During its tenure, the institute supported long-term studies of cougars, brown and black bears, jaguars, tigers, and snow leopards as well as shorter-term studies of other carnivores (Koehler and Hornocker 1989, 1991; Quigley and Crawshaw 1992; Miquelle et al. 1995, 1996a, 1996b; Murphy 1998; Ruth 2004a; Ruth et al. 1998; Logan and Sweanor 2001; Kerley et al. 2003; Seryodkin et al. 2003; Costello 2008; Costello et al. 2008, 2009; Goodrich et al. 2008).

In the early to mid-1980s, as signs of cougars in Yellowstone National Park increased and plans to restore wolves were in development (US Fish and Wildlife Service 1978; National Park Service 1990; Varley and Brewster 1992), Hornocker realized there was a critical gap in information: how would wolf recovery influence cougar populations, predation by cougars, and existing conservation and management of the large American cat? He also recognized an opportunity: to conduct a long-term, intensive study on cougars that would take advantage of a natural experiment as wolf restoration became a reality in the Greater Yellowstone Ecosystem. A first step was to survey the Greater Yellowstone Northern Range and determine study feasibility. In cooperation with Yellowstone National Park and the Montana Department of Fish, Wildlife and Parks, the Hornocker Wildlife Institute conducted track surveys across the Northern Range of Yellowstone and adjacent lands north of the park boundary. Results of this survey, carried out in the winter of 1985–86, confirmed that a number of cougars did indeed inhabit the northern winter range, indicating recovery from very low numbers prior to cessation of poisoning and implementation of hunting regulations. Spurred by the track survey findings, Hornocker approached Superintendent Robert Barbee and John Varley, then director of the Yellowstone Center for Resources, about conducting a long-term study. The study goals were straightforward: to document the ecology of cougars in the northern Yellowstone system and lay the foundation of sound information on cougars prior to the planned restoration of wolves. This foundational work, from 1987 to 1994, was overseen by Hornocker and undertaken

by Kerry Murphy through the University of Idaho, resulting in his doctoral dissertation, “The Ecology of the Cougar (*Puma concolor*) in the Northern Yellowstone Ecosystem: Interactions with Prey, Bears, and Humans” (1998).

The restoration of wolves to Yellowstone and Idaho’s River of No Return Wilderness became a reality in 1995 and 1996, with the success of the restoration quickly surpassing expectations for wolf recovery (Fritts et al. 2001). With the restoration of wolves to the Greater Yellowstone Ecosystem, the four largest North American carnivores—wolf, grizzly bear, black bear, and cougar—were once again sympatric in the system. Prior to the restoration of wolves in Idaho, Montana, and Wyoming, the Northern Continental Divide Ecosystem—including Glacier National Park, which wolves had naturally recolonized in the late 1970s to early 1980s—was the only area supporting a complete assemblage of large carnivores in the contiguous forty-eight states (US Fish and Wildlife Service 1978; Apps et al. 2007). Noting the unmatched opportunities these two systems provided to gain knowledge about the influence of carnivores on one another and on ungulate prey, Hornocker initiated studies in the Glacier area in 1993 (Ruth 2004a) and later in Yellowstone, with a second-phase cougar study following the restoration of wolves. In late winter 1998, lead field scientist Toni Ruth began marking cougars, and soon afterward Polly Buotte joined the team to serve as geographic information specialist and coordinator of field crews quantifying cougar kill rates and displacement of cougars from their kills. In 2000 the Hornocker Wildlife Institute merged with the Wildlife Conservation Society, known for its international work to save wildlife and wild places. Our work continued under the Hornocker Wildlife Institute/Wildlife Conservation Society program through the end of our study in 2006.

Wolf restoration also led to other new multi-predator and multi-prey studies (Kunkel et al. 1999; Husseman et al. 2003b; Ruth 2004a; Kortello et al. 2007). These studies lasted two to four years and lacked data on cougars prior to wolf restoration, therefore relying on comparisons between cougar and wolf diets, selection of prey, spatial overlap, habitat use, and population dynamics to gain understanding of predatory roles and competition. Notably then, grounded in seven years of data on cougar ecology prior to wolves, our study was the first long-term investigation of cougar-wolf interactions and the first opportunity to conduct such research within the framework of a natural experiment—wolf restoration.

Fundamental to our investigation of species interactions and the large carnivore community in Yellowstone were: (1) committing to a long-term effort with a robust field presence and (2) forming strong collaborations with other established and committed research efforts on carnivores and prey. Including the work of Murphy (1998), our efforts translated into more than 7,000 person-days of fieldwork on cougars over sixteen years, 11,950 ground and aerial VHF locations, 19,530 GPS locations, 744 cougar kills, more than 22,500 kilometers of winter population tracking transects, and repeated blood, tissue, and hair samples from 163 cougars for disease and genetic studies. In addition, our efforts occurred in the midst of long-term studies and data accrued on bears (Interagency Grizzly Bear Study Team; see <http://www.nrmcs.usgs.gov/science/igbst/detailedpubs> for publications) and on wolves, coyotes, ungulates, and vegetation changes on the Greater Yellowstone Northern Range. Numerous graduate projects and publications have resulted from the diverse array of questions addressed within the system (see <http://www.greateryellowstonescience.org> for publications). As a result, we collaborated with other researchers and often had access to pertinent databases and expert knowledge from various federal and state agencies and university scientists that provided crucial insights into the strengths and weaknesses of the various sets of data (Ruth et al. 2003; Mao et al. 2005; White et al. 2007; Cross et al. 2009; see also Garrett et al. 2009b).

We were particularly fortunate to have two colleagues, Dr. Kerry Murphy and Dr. Doug Smith, employed at Yellowstone National Park during our study. In addition to Kerry's study on cougars prior to wolf restoration providing the groundwork and framework for our post-wolf restoration study, he also granted us access to his entire data set collected while he worked as a Hornocker Wildlife Institute scientist. Having such thoroughly collected data in hand is a wonderful thing. Yet we were limited in its use by the layers of details that do not come with paper or digital data records—details acquired through Kerry's experiences spending every day collecting data in the field (fig. 1.2). His knowledge of the individual animals he radio-collared and followed and of the landscape and climate at a particular time is his alone. Our privilege and benefit were to have his scientific background, ideas, and input on these hidden details throughout the post-wolf restoration study.



**FIGURE 1.2.** Kerry Murphy uses radio-telemetry to locate a cougar on the Greater Yellowstone Northern Range. Kerry led the study on cougars prior to wolf restoration, providing the groundwork and data for comparing cougar ecology following the restoration of wolves. Hornocker Wildlife Institute photo.

Doug Smith was in Yellowstone when the first wolves were brought into the soft-release pens and eventually released from those pens. He has coordinated population monitoring and numerous research studies as Yellowstone Wolf Project leader since 1995, resulting in well over ninety peer-reviewed publications (see [http://www.greateryellowstonescience.org/search/apachesolr\\_search/wolf%20publications](http://www.greateryellowstonescience.org/search/apachesolr_search/wolf%20publications)). Throughout our post-wolf restoration project, Doug was an enthusiastic, insightful, and supportive associate and collaborator. Field coordination, communication, and assistance with ground and aerial monitoring between our projects yielded valuable shared information on interactions between cougars and wolves. Kerry and Doug are contributing authors of chapters 5, 6, 11, and 15 of this book.

We also established a strong relationship with Chuck Schwartz and Mark Haroldson of the Interagency Grizzly Bear Study Team and, along with Yellowstone National Park Bear Management Specialist Kerry Gunther and Doug's wolf project, our three study teams addressed specific multi-carnivore questions coordinated through formation of the Large Carnivore Working Group in August 1998 (fig. 1.3). Led by Howard Quigley, the Large Carnivore Working Group focused on the Northern Range of Yellowstone National Park. This area was chosen because of the coexistence of





**FIGURE 1.3.** To understand the interactions among cougars, wolves, and bears, the Large Carnivore Working Group formed in August 1998. Left to right: Mark Haroldson, Doug Smith, Polly Buotte, Steve Cherry, Chuck Schwartz, Howard Quigley, Kerry Gunther, Toni Ruth, and Dan Stahler (Haroldson and Schwartz—Interagency Grizzly Bear Study Team; Smith, Gunther, and Stahler—Yellowstone National Park; Buotte, Quigley, and Ruth—Hornocker Wildlife Institute/Wildlife Conservation Society; Cherry—Montana State University).

grizzly bears, wolves, cougars, and black bears and the presence of our active field-based research and monitoring projects. With much of the single-species research already under way, the group concentrated on ways of integrating databases for a systems approach to natural resources management, giving added scientific and conservation value to individual projects by working together to understand the interactions among the large carnivores (e.g., Ruth et al. 2003).

Our intent in synthesizing our research in a book was to provide objective scientific data at the forefront of understanding cougars and large carnivore community struc-

ture and management issues in the Greater Yellowstone Ecosystem and elsewhere where wolves and cougars are being restored. We would like to emphasize that the findings presented apply to a particular period in a specific study area. Wildlife populations do not remain static, and ecosystems vary over time (Schaller 1972). As more studies investigate interspecific interactions and the role they play in various ecosystems, some of our findings may hold, others may be drawn into question, and new questions that advance our understanding of multi-species interactions in structuring communities will be answered.

## CHAPTER 2

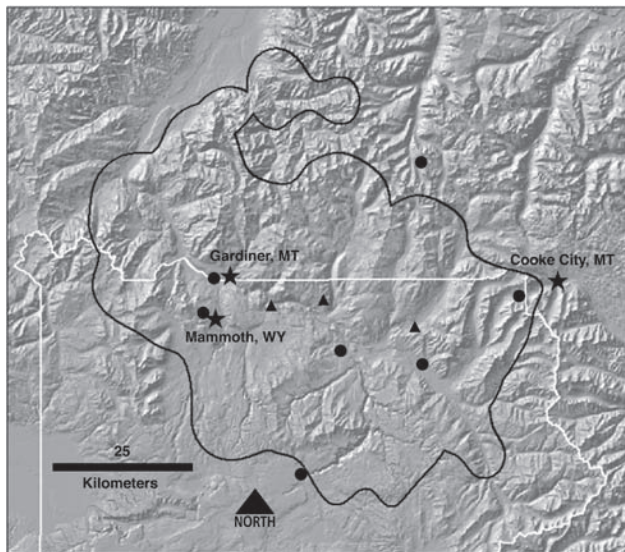
### The Northern Yellowstone Landscape

Both Yellowstone and Grand Teton National Parks lie within the 56,000 km<sup>2</sup> that comprise the Greater Yellowstone Ecosystem in Wyoming, Montana, and Idaho. Federal lands comprise 76 percent of the area (Smith and Bangs 2009). In addition to the two national parks, the region encompasses seven national forests, three national wildlife refuges, Bureau of Land Management holdings, and a mosaic of state and private lands. Seven recognized floras converge in the Greater Yellowstone Ecosystem: the Southern Rocky Mountain, Pacific Northwest, Northern Rocky Mountain, Boreal North American, Boreal Circumpolar, Arctic, and Great Basin (Clark and Minta 1994). The Greater Yellowstone Ecosystem straddles the Continental Divide and includes the headwaters of three major river systems: the Yellowstone-Missouri, the Green-Colorado, and the Snake-Columbia Rivers. The Yellowstone is the longest free-flowing river in the lower forty-eight states, providing habitat for diverse wildlife and fish populations (McBride and Nickerson 2006). A vast volcanic plateau with average elevations around 2,440 meters (8,000 feet), the Greater Yellowstone area experiences 1,000 to 3,000 earthquakes annually and contains more than 10,000 hydrothermal features providing sources of heat that are important to wildlife during winter (Clark and Minta 1994; Yellowstone National Park 2008; Garrott and White 2009).

The diverse landscape represents one of the largest intact temperate ecosystems remaining on the planet and the most nearly intact complex of wilderness, wild ungulates, and large carnivores in the lower forty-eight states (Smith et al.

2004a; Garrott and White 2009). Historically and at present, Yellowstone's ungulate biomass supports populations of large carnivores. Fossil fauna in Lamar Cave, a late Holocene paleontological site in Yellowstone National Park, yielded thirty-six fossil mammalian species that are similar to the mammals in the park today, including fossils of wolves, coyotes, bears, and bobcats (Barnosky 1994; Hadly 1990, 1999). Although the cave yielded no cougar fossils, along with the other carnivores, cougars occupied Yellowstone National Park (Schullery and Whittlesey 1999). In addition to an abundance of large mammal species with strong ecological influences, humans have had a long presence in the region as well, spanning more than 12,000 years.

Today the Greater Yellowstone Ecosystem is part of a growing human community in which people are having an increasing impact on both sides of the park boundary (Wright Parmenter et al. 2003). The region's population has grown steadily over the past several decades. Coupled with this growth has been a change in demography and a change from ranching and farming to urban and exurban development (Hansen 2009). While Greater Yellowstone experienced a 58 percent increase in population from 1970 to 1999, the area of rural lands supporting exurban development increased 350 percent during that period (Hernandez 2004; Gude et al. 2006). Along with rural residential development, recreation in the area has also increased as people are attracted to the natural amenities (Hansen et al. 2002; McBride and Nickerson 2006). Since 1992 approximately 2.8 million to 3.1 million people have visited Yellowstone



**FIGURE 2.1.** The 3,779 km<sup>2</sup> Greater Yellowstone Northern Range study area (black line), overlapping Yellowstone National Park (white line), Montana, and Wyoming. Climatological sites (circles) providing temperature, rain, and snowfall data were distributed across the study area. Yellowstone National Park provided access to cabins (triangles) that enabled us to remain in the field for days at a time during our remote winter work.

National Park each year, with most visitations occurring in summer, and roughly 14.5 million have explored the Greater Yellowstone Ecosystem each year and used it for recreation (Varley and Brewster 1992; Clark and Minta 1994; [www.greateryellowstonescience.org](http://www.greateryellowstonescience.org) 2009). An unexpected result of wolf recovery, the high visibility of wolves across the Northern Range has generated even greater national and international public interest in coming to Yellowstone to observe wolves and experience the park.

### NORTHERN YELLOWSTONE STUDY AREA

Our study area of approximately 3,779 km<sup>2</sup> at the northern end of Yellowstone and overlapping the northern park boundary—shown in figure 2.1—encompassed the broad grassland bordering the Yellowstone and Lamar Rivers and known as the northern ungulate winter range (approximately 1,520 km<sup>2</sup>; Houston 1982; Lemke et al. 1998; P. J. White et al. 2010). Fifty-seven percent of our study area fell within the Northern Range and inside Yellowstone National Park, with the remainder of the study area to the

north of the Yellowstone boundary, including portions of the adjoining Absaroka-Beartooth Wilderness and the Gardiner Basin.

The Greater Yellowstone Northern Range study area was chosen for several reasons. First, it served as critical winter range for a large ungulate population, and cougars naturally recolonized the area by the late 1970s to early 1980s (Murphy 1998). Second, as a result of deep snow accumulations and few winter prey other than bison in the central portion of Yellowstone, the Northern Range supported a year-round cougar population, while cougars used more central areas of the park primarily during summer. Third, the elk-rich northern winter range served as the primary release site for wolf restoration in 1994 and 1995 (Smith and Bangs 2009). Since their restoration, the Northern Range wolves have been intensively and consistently studied. Long-term data sets on population characteristics, pack structure and dynamics, predation, and population genetics have accumulated; and numerous scientific articles, graduate theses, and dissertations have been produced (Smith et al. 2008; Smith and Bangs 2009).

Elevations rise from about 1,500 meters along the Yellowstone River near Gardiner to more than 2,900 meters at the eastern end of the study area near where Soda Butte Creek and Slough Creek flow into the Lamar River, which then merges with the Yellowstone River (Despain 1990; DelGiudice et al. 2001; R. C. Cook et al. 2004). Within Yellowstone National Park, other major drainages that flow into the Yellowstone River include Tower Creek, Hellroaring Creek, Cottonwood Creek, Blacktail Deer Creek, Crevice Creek, and the Gardiner River. The landscape pattern is complex along the network of creeks, rivers, and valleys, consisting of meadow systems interspersed with topographically rugged and rocky terrain. River canyons frequented by cougars are steep, with slopes typically between 26 and 50 degrees (fig. 2.2).

Gardiner, Montana, a small town situated on Yellowstone's northern boundary with a year-round population of 800 people, served as our base of operations during both study phases: to the presence of wolves and during wolf restoration, hereafter referred to as the PW and DW studies (fig. 2.3). The Northern Range study area was accessible year-round by one paved road extending from Gardiner to Cooke City, Montana. Thus most of our work was conducted on foot, and we hiked during all seasons and snowshoed when snow depth dictated.





**FIGURE 2.2.** Polly Buotte (foreground), Brad Schultz, and hounds Dillon and Pip navigate through prime cougar habitat along the steep, south-facing slopes above the Yellowstone River. Photo by Toni Ruth, Hornocker Wildlife Institute/Wildlife Conservation Society.

### Soils, Climate, and Vegetation

Yellowstone's location between the 44th and 45th parallels, halfway between the equator and the North Pole, greatly influences the climate and resulting vegetation (Despain 1990). The Yellowstone we see and try to understand today is a visible representation of geological, climatological, and biological forces and events (Meagher and Houston 1998). As such, it is a complex system.

Two distinct parent materials for soils predominate in Yellowstone, which influence mineral nutrients and moisture available for plant growth (Despain 1990). Andesitic volcanic rock was laid down around 70 million to 80 million years ago, and rhyolitic volcanic rocks were laid down between 2 million and 76,000 years ago. The extensive lodgepole pine forests of the Yellowstone Plateau reflect the underlying nutrient-poor soils derived from the rhyolite lava flows of the Yellowstone caldera (Meagher and Houston 1998). In contrast, the more productive Northern Range soils were derived largely from andesitic rocks, in which

calcium is about ten times more abundant and carbon three times more abundant than in rhyolitic soils (Despain 1990; Meagher and Houston 1998). As Despain (1990: 150) noted, "It is no coincidence that the summer ranges used most heavily by ungulates and where grizzly bears spend most of their foraging time are in vegetation associated with andesitic substrates."

Yellowstone National Park has two contrasting climatic regimes: a dry summer/wet winter climate prevails in the southern and central areas of the park, and wet summer/dry winter conditions prevail in the north (Meagher and Houston 1998). The climate of the Northern Range consists of generally long, cold winters and short, cool summers (Houston 1982; Despain 1990; Meagher and Houston 1998). Spring typically begins in April, with melting snow, cool to cold nights, and warm to cool days, and extends through June. Summer—July and August—is characterized by warm days, frequent thunderstorms, and infrequent freezing nighttime temperatures. By fall, September to late October, nighttime temperatures drop to freezing and the day temperatures are warm to cool. Arriving in mid- to late October and lasting into early April, winter is characterized by maximum temperatures frequently below freezing and by the accumulation of snow.

The two main differing weather regimes, along with an elevational climatic gradient, influence vegetation patterns—mountainous sites receive more precipitation and are cooler than valley sites. Historical climate recordings extend from 1949 to the present, providing data from ten climatological stations situated in and adjacent to Yellowstone National Park (Farnes et al. 1999). Four of the stations are distributed across the Northern Range at Gardiner, Montana, and in Wyoming at Mammoth, Tower Falls, and in the Lamar Valley (see fig. 2.1). Daily precipitation, maximum and minimum air temperatures, snowfall, and depth of snow on the ground are collected manually at these sites. Around 1975 to 1980, remote snow-monitoring equipment was installed at higher elevations. These SNOWTEL sites make year-round precipitation and air temperature information available from areas within and adjacent to the park (Despain 1990; Farnes et al. 1999).

Mean annual temperatures varied substantially across our study years, 1987 through 2005 (fig. 2.4a, b). December was the coldest month (mean temperature of  $-10.5 \pm 2.6^{\circ}\text{C}$  at Tower Falls) and July was the hottest month (mean temperature of  $14.4 \pm 1.9^{\circ}\text{C}$  at Tower Falls) during the PW study

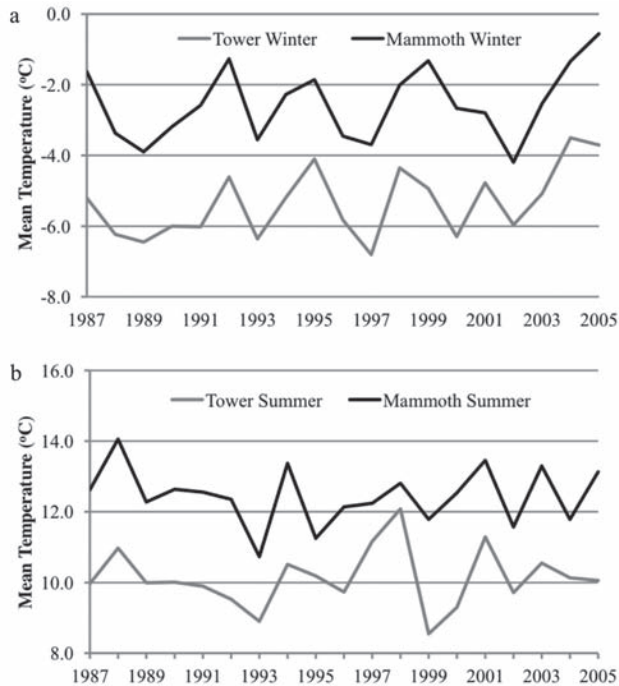




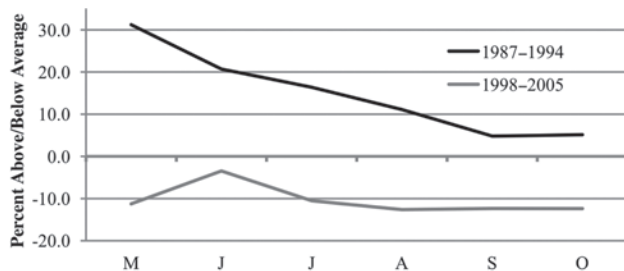
**FIGURE 2.3.** Looking southeast from Sepulcher Mountain toward the town of Gardiner, Montana. Serving as the gateway to the north entrance of Yellowstone National Park, Gardiner was our home and served as our base of operations during the PW and DW cougar studies. Photo by Tyler Coleman, Hornocker Wildlife Institute/Wildlife Conservation Society.

years. During wolf restoration, January was the coldest month (mean temperature of  $-8.3 \pm 1.4^{\circ}\text{C}$  at Tower Falls) and July the hottest month (mean temperature of  $16.1 \pm 1.5^{\circ}\text{C}$  at Tower Falls). Nearly 50 percent of the total annual precipitation is in the snowpack on the first of April and is released into the soil and surface waters over the next three months before soils dry out during the summer (Despain 1990). Consequently, in years of low winter precipitation, drought conditions usually prevail (Despain 1990). Our post-wolf restoration study was characterized by slightly milder winters but more so by summer rainfall that was consistently 4 percent to 12 percent below average, reflecting drought conditions (fig. 2.5).

Winter temperature and snow cover combine to limit the access of large herbivores to winter forage; consequently, both summer and winter conditions set upper limits to prey population sizes in the park (Meagher and Houston 1998). By combining monthly precipitation and temperature records, Farnes and colleagues (1999) produced a relative winter severity index (WSI) to provide a measure of winter influences on ungulate species. Values above zero (all positive WSI values) typically indicate low winter kill and good reproduction and recruitment. As a consequence, carnivores work harder to obtain prey when winter severity is low and favorable for ungulates (Farnes et al. 1999). At values between  $-1.0$  and  $-2.0$ , ungulates show some reduc-

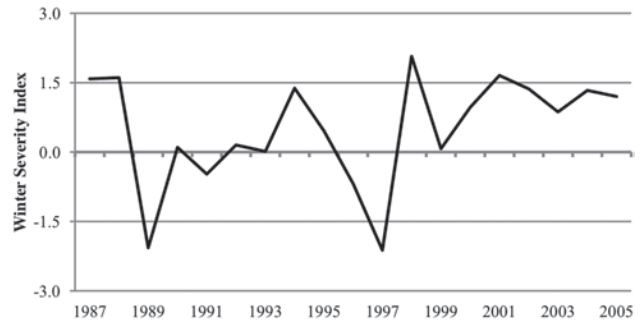


**FIGURE 2.4.** Annual temperature trends in °C for winter (a) and summer (b), from climatological stations at Tower Falls and Mammoth, Wyoming, on the Northern Range study area, 1987–2005.



**FIGURE 2.5.** Average monthly rainfall presented as percent above or below the forty-seven-year monthly average for the period 1958–2005 (zero axis). Precipitation data were averaged from climatological stations at Tower Falls and Mammoth, Wyoming. Above-average precipitation characterized the pre-wolf restoration study phase, 1987–1994, and during the wolf restoration study phase a drought persisted from 2001 through 2005.

tion in reproduction but typically little mortality of older animals and yearlings. Winter severity index values below  $-2.0$  tend to indicate significant mortality, low reproduction rates, and weaker calves and lower birth weights. More animals may die than enter the population; hence herd recruit-



**FIGURE 2.6.** Average winter severity index (WSI) calculated for elk on the Greater Yellowstone Northern Range, Yellowstone National Park and Montana, 1987–2005 (procedure documented in Farnes et al. 1999). Values above zero (positive WSI), indicating mild winter conditions, were present during all years of the post-wolf restoration study, 1998–2005.

ment rates are low or even negative. In addition, the reduced condition and increased vulnerability of ungulates makes it easier for carnivores to subdue and kill them and also provides increased scavenging opportunities as ungulates die from starvation. Between 1888 and 1990, the winter severity index on Yellowstone's Northern Range not only demonstrated striking annual variability but suggested a trend toward comparatively milder winters (see fig. 14 in Meagher and Houston 1998: 225–26). Our two study periods similarly reflect annual variability, and the winters of 1998–2005, with average winter severity indices consistently above zero, reflect milder winters (fig. 2.6) than those during the PW study of 1987–94.

Within the Northern Range, the large valleys of the Yellowstone and Lamar Rivers occupy about 9 percent of the area (Despain 1990). Topography of the valley bottoms is undulating, often with contorted drainages resulting from glacial depositions. Most of the area is covered by nonforest vegetation types—primarily grassland and sagebrush steppe at lower elevations, dominated by Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and big sagebrush (*Artemisia tridentata*). Big sagebrush covers about 37 percent of the area. The montane forest also includes Douglas-fir (*Pseudotsuga menziesii*)—mostly of the Douglas-fir/snowberry or Douglas-fir/pinegrass types (Despain 1990)—and lodgepole pine (*Pinus contorta*), together covering about 41 percent of the Northern Range (Houston 1982; Wright et al. 2006).

Fire is an important part of disturbance, vegetative succession, and patterns of forage availability in the Yellowstone ecosystem (Despain 1990; Meagher and Houston 1998). Through most of the twentieth century, natural fires were suppressed in Yellowstone until the policy changed in 1972 (Varley and Schullery 1991; Yellowstone National Park 2008). Following the 1972 policy change, fires ignited by lightning in remote areas were allowed to burn, thus restoring natural fires to the Greater Yellowstone Ecosystem (Schullery 1989; Clark and Minta 1994; Despain 1990). As we collected data on cougars after wolf restoration, a total of nine fires burned roughly 344 km<sup>2</sup>, or 9 percent, of the study area. Prior to wolf restoration, eight fires occurred, but the most significant fire event took place a year after the study got under way. In 1988 fires burned more than 3,200 km<sup>2</sup>, including about 50 percent of forested areas in the park and 38 percent, or 1,451 km<sup>2</sup>, of our study area. The 1988 burn affected roughly 30 percent of the summer range and 32 percent of the winter range for the northern Yellowstone elk herd, and cover for all ungulate species was dramatically affected (Singer and Mack 1999). Although little of their winter range burned, mule deer declined 19 percent and pronghorn declined 29 percent. Elk mortality rose to about 40 percent in the winter of 1988–89, yet elk numbers then rapidly increased because of abundant plant growth in the first three years after the fire.

### The Grazers and Other Fauna

Nine genera of large browsers and grazers that were present in the Pleistocene survived to the present day (Pielou 1991). Seven of these genera represented by eight species of ungulates—elk, bison, mule deer, moose, bighorn sheep, pronghorn, white-tailed deer, and mountain goat—are still present in and adjacent to Yellowstone. At times numbering more than 95,000 individuals, they constitute the largest concentration of hoofed animals in any area of comparable size in North America (Singer and Mack 1999; Smith and Bangs 2009). The largest single concentration of ungulates in the Greater Yellowstone Ecosystem occurs on the northern Yellowstone winter range, where populations of six ungulates are found at densities of nineteen to twenty-one ungulates per square kilometer (Singer and Mack 1999: 189). The substantial biomass of ungulates is roughly twenty-two times more abundant than the biomass of all non-ungulate mammalian prey combined. Having a profound influence on the vegetation in Yellowstone National Park and surround-

ing lands, herbivory by large mammals—particularly elk and bison—and smaller species, including beavers, pocket gophers, and insects, is visible in photo comparisons made by Meagher and Houston (1998).

Numerically, elk (*Cervus elaphus*) outnumbered all other ungulates during our studies by a ratio averaging 6 to 1 and were more likely than other ungulates to influence vegetation, regulate ecosystem processes, and provide food for large carnivores (fig. 2.7; Singer and Mack 1999). Elk occupied all vegetation types in the park at some season of the year. Elk and mule deer (*Odocoileus hemionus*) were the most abundant ungulate prey for cougars and wolves (Murphy 1998; D. W. Smith et al. 2004a, 2004b; Smith 2005). The minimum counts for these key prey species were 9,400–19,000 elk and 1,600–2,500 mule deer prior to wolves (1987–94; Lemke et al. 1998; Murphy 1998). Elk numbered 8,300–14,500 and deer 1,600–2,300 after wolf restoration (1998–2005; Smith et al. 2004a; White and Garrott 2005; Cross et al. 2009).

Most ungulates migrated seasonally between summer and winter ranges (Craighead et al. 1972; Houston 1982; Singer and Mack 1999; White et al. 2010). The bulk of elk migrated from restricted low-elevation winter ranges to expansive high-elevation summer ranges located along hydrographic divides (Meagher and Houston 1998; White et al. 2010). Female elk typically showed fidelity to travel routes and returned to specific areas of summer and winter ranges in successive years, yet other elk showed flexibility from year to year, sometimes moving to different summer ranges throughout the park (White et al. 2010). In general, there were two herd segments in the northern Yellowstone population—Lamar River Valley and Yellowstone River Valley—with additional elk varying their migration strategies in response to weather conditions (Craighead et al. 1972; Hamlin 2006; Hamlin et al. 2009a; White et al. 2010).

Timing of migrations varied annually (White et al. 2010). Elk delayed spring migration after winters with high snowpack and migrated earlier in years with lower snowpack and earlier vegetation green-up. Elk departed from summer ranges at similar times, but those elk traveling to winter ranges outside the park were found to delay arrivals to winter range, likely to avoid risk of death from hunting by humans (White et al. 2010). During winter, elk were well distributed throughout the Northern Range, but nearly all the mule deer migrated north and resided in the Gardiner Basin, with fewer than 100 remaining within Yellowstone National Park





**FIGURE 2.7.** Serving as the main food of cougars and wolves, elk outnumbered other ungulates by a ratio averaging 6 to 1 and occupied all vegetation types in the park at some season of the year. Photo by Jason Husseman, Hornocker Wildlife Institute/Wildlife Conservation Society.

(Murphy 1998; Yellowstone National Park 2008). Thus mule deer were typically available as prey to only a few cougars and wolves in the study area during much of winter.

During the 1970s and 1980s, the northern Yellowstone elk population expanded its winter range north of the park and into the Paradise Valley of Montana in response to changes in the structure and timing of hunter harvests, increasing elk abundance, protection of winter ranges outside the park, and the extensive fires of 1988 (Coughenour and Singer 1996b; Lemke et al. 1998). As a result, the estimated carrying capacity increased to between 20,000 and 25,000 elk (Taper and Gogan 2002).

In addition to elk and mule deer, 125 to 225 bighorn sheep (*Ovis canadensis*), 700–1,000 pronghorn antelope (*Antilo-*

*capra americana*), fewer than 200 moose (*Alces alces*), 100 mountain goats (*Oreamnos hemionus*), and small numbers of white-tailed deer (*O. virginianus*) were present on the study area (D. W. Smith et al. 2004a) and were occasionally killed by cougars. Mountain goats are non-native to Yellowstone but have colonized the northwestern and northeastern portions of the park. Bison (*Bison bison*) numbered 2,000–4,000 but were not cougar prey (fig. 2.8; Murphy 1998). With the exception of occasionally killing bighorn sheep and mountain goats, wolves preyed on elk, deer, moose, bison, and pronghorn (Smith et al. 2005, 2008).

In addition to ungulates, cougars and wolves interacted with other animals present on the Greater Yellowstone Northern Range. Common ravens (*Corvus corax*), black-



**FIGURE 2.8.** Although bison numbered 2,000–4,000 and we encountered them in low-elevation cougar habitat—such as this one pictured near the junction of Blacktail Deer Creek and the Yellowstone River—they were not cougar prey during the pre-wolf or during wolf studies. Photo by Polly Buotte, Hornocker Wildlife Institute/Wildlife Conservation Society.

billed magpies (*Pica hudsonia*), and bald and golden eagles (*Haliaeetus leucocephalus* and *Aquila chrysaetos*) were frequent scavengers of cougar and wolf kills. We occasionally documented golden eagles, Northern saw-whet owls (*Aegolius acadicus*), and blue grouse (*Dendragapus obscurus*) as cougar food. Along with wolves and bears, coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) also scavenged cougar kills (Ruth et al. 2010). We occasionally encountered tracks of bobcats (*Lynx rufus*) and wolverine (*Gulo gulo*) but only in specific locations of our study area. Wolverines did not frequent the low-elevation sagebrush habitats predominant on the Northern Range and, along with lynx (*Lynx canadensis*),

were considered rare in Yellowstone. Research completed in 2004 confirmed the presence of lynx in the central and eastern portions of the park (Murphy et al. 2006). We more frequently saw tracks of and occasionally observed badgers (*Taxidea taxus*), river otters (*Lutra canadensis*), martens (*Martes martes*), and long- and short-tailed weasels (*Mustela frenata* and *M. erminea*).

Thirty-one species of small mammals of three orders (Yellowstone National Park 2008) resided in Yellowstone, and several were potential cougar and wolf prey, primarily during summer. The most common were yellow-bellied marmot (*Marmota flaviventris*), Uinta ground squirrel



(*Spermophilus armatus*), golden-mantled ground squirrel (*S. lateralis*), red squirrel (*Tamiasciurus hudsonicus*), porcupine (*Erethizon dorsatum*), snowshoe hare (*Lepus americanus*), white-tailed jackrabbit (*L. townsendii*), desert cottontail (*Sylvilagus audubonii*), mountain cottontail (*S. nuttallii*), chipmunks (*Tamius minimus*, *T. umbrinus*, and *T. amoenus*), and beaver (*Castor canadensis*).

Past glacial activity and cool, dry conditions predominant for much of the year are likely responsible for the relatively low diversity of reptiles and amphibians inhabiting Yellowstone. Prairie rattlesnakes (*Crotalis viridis viridis*) were one of the six species of reptiles that inhabited the park (Yellowstone National Park 2008), and during summer we frequently encountered these snakes in mixed open woodland, on the sagebrush steppe, on rocky slopes along the Black Canyon of the Yellowstone near Gardiner, and in the Gardiner Basin. One young cougar died following his encounter with a prairie rattlesnake.

## WILDLIFE MANAGEMENT ON THE NORTHERN RANGE

Similar to other portions of the ecosystem, the Northern Range spans the jurisdictions of several federal and state agencies, so different portions of the area are managed according to diverse policies and land use practices. These sometimes disparate management structures primarily affect migratory animals such as ungulates and the carnivores that rely on them, many of which winter in lower-elevation areas on the public-private land interface.

### History

Yellowstone was established to protect its unusual geological and thermal features and areas of exquisite beauty and cultural value, allowing for their enjoyment by current and future generations (Schullery and Whittlesey 1999). The National Park Service is mandated to manage Yellowstone in as natural a state as possible (Despain 1990). Yet Yellowstone's history is similar to that elsewhere in the United States regarding predators—they were viewed as a threat to human safety and livestock and as having negative impacts on game species such as elk and deer. Yellowstone National Park's official involvement with predator control lasted from 1914 until 1936, after which park predator control programs were largely curtailed (Schullery and Whittlesey 1999). Largely as a result of these predator control programs, wolves were

eradicated by the 1930s (Mech 1970; Weaver 1978; Bangs et al. 1998), and cougar numbers were greatly reduced (Young and Goldman 1946; Schullery and Whittlesey 1999). The last reported official killing of a cougar in Yellowstone occurred in 1925, and the National Park Service ceased predator control in 1935 (Johnston 2002: 19).

Following carnivore removal, wolves were absent and few cougars were observed in Yellowstone for forty to fifty years. While numbers of game animals and predators slowly began to rise between the 1930s and the 1980s, cougars continued to be killed outside the park under bounty management until state seasons and quotas were implemented in the early 1970s (Trefethen 1975; Riley et al. 2004; Gill 2009). Although it is unclear whether they were completely extirpated from the park or reestablished themselves from elsewhere, by 1987 cougar numbers were on the increase in northern Yellowstone (Murphy 1998).

In 1973, following the closures of garbage dumps and the subsequent controversy surrounding the status of the grizzly bear population, the US Department of the Interior formed the Interagency Grizzly Bear Study Team (Knight et al. 1999), a cooperative effort among the US Geological Survey, National Park Service, US Forest Service, US Fish and Wildlife Service, and the states of Idaho, Montana, and Wyoming. Grizzly research and management in greater Yellowstone intensified after the 1973 establishment of the interagency study team. In 1975 the grizzly bear in the contiguous forty-eight states was listed as threatened under the Endangered Species Act, which resulted in cessation of grizzly bear hunting. Today, the study team continues to monitor population numbers and trends and to provide better understanding of bear food habits and behavior in relation to humans and to other wildlife species (Schwartz et al. 2006a, 2006b).

Much less is known about the park's black bears. Only one black bear population study has occurred in a portion of the park (Barnes and Bray 1967). Although there are no current scientific estimates of the black bear population in the Greater Yellowstone Ecosystem, black bears are considered common. Radio-collaring of a small number of black bears initiated by Yellowstone National Park and the Interagency Grizzly Bear Study Team in 2000 is lending insight into habitat use and movements of black bears on the Northern Range.

Controversy about management of the large ungulate population and concerns about overgrazing and over-

browsing have been some of the central issues regarding the Northern Range for more than eighty years (Houston 1982; Meagher and Houston 1998; Yellowstone National Park 2008). For an extended period, from 1935 to 1968, concerns about overgrazing and overbrowsing resulted in more than 26,000 elk being shot or shipped out of the park to control ungulate numbers. Hunting outside the park removed another 45,000 elk during this period. Park managers ended the removal program in 1969, and the elk population increased from 12,000 to more than 25,000 by 1988, accentuating the debate regarding the effects of elk grazing on the Northern Range (Houston 1982; Meagher and Houston 1998; Eberhardt et al. 2007).

### **Influences during Our Study**

Because hunting elk is culturally and economically important to people in areas surrounding Yellowstone, increasing wolf numbers after restoration changed the debate from concerns about too many elk and overgrazing to concerns about a roughly 8 percent annual decline in elk numbers and an approximately 50 percent overall elk decline during the period 1995–2005 (White and Garrott 2005; Cross et al. 2009; Smith and Bangs 2009). In addition to predation by wolves and other large carnivores, several other factors contributed to this decreasing trend in elk numbers during the years 1995–2005: human harvests of antlerless elk during the Gardiner late elk hunt, possible drought effects on elk maternal condition and recruitment, increased use of winter range north of the park boundary, and winterkill (Vucetich et al. 2005; White and Garrott 2005; Varley and Boyce 2006; Barber-Meyer et al. 2008; Hamlin et al. 2009a).

Our study area overlapped Montana hunting unit 313 and the southern portion of unit 314 to the north of Yellowstone National Park. Elk that migrated out of the park were legally hunted from September through February during four hunts—archery season, early season backcountry, general autumn hunt, and the Gardiner late elk hunt—which were managed by the Montana Department of Fish, Wildlife and Parks (White and Garrott 2005; Cross et al. 2009). Bull elk were the primary focus of hunters during the archery, early season backcountry, and general autumn hunts from September through November. The Gardiner late elk hunt was established as a special limited-access management tool designed to harvest northern Yellowstone elk that migrate into Montana (Cross et al. 2009). Since 1976 this hunt has

had two primary objectives: (1) to help regulate the number of elk that winter north of Yellowstone National Park at levels that will maintain winter range habitat on a long-term sustainable basis without reducing forage productivity or plant species diversity and (2) to harvest elk in ways that will minimize the effect of hunting on migratory behavior, allowing traditional elk winter use to be distributed over the winter range in proportion to forage availability (Cross et al. 2009). To accomplish these objectives, the hunt was heavily biased toward harvesting females so that elk numbers would not exceed the carrying capacity of the winter range and cause long-term changes in plant communities or declines in forage production.

The harvest of elk was not initially reduced following wolf restoration to compensate for additional offtake by wolves but was instead maintained between 2,660 permits in 1995 and 2,882 permits in 2000 (White and Garrott 2005). Deep snow influenced elk migration outside the park such that a relatively constant proportion—about  $27 \pm 5$  percent—of elk were harvested regardless of elk density (White et al. 2003; White and Garrott 2005). Hunter success exceeded 95 percent during years with high levels of snow water equivalent, compared to hunter success of 64 percent averaged over all years from 1976 through 2005. As a result of decreases in elk abundance and elk migration north of Yellowstone National Park, the number of antlerless elk permits was steadily decreased to 1,400 permits in 2004, resulting in a total harvest of 6 percent of the estimated population. To reduce hunter mortality on female elk further, the Montana Department of Fish, Wildlife and Parks reduced the number of antlerless permits for the Gardiner late elk hunt from 1,102 in 2005 to about 100 per season during the period 2006–2008 (Cross et al. 2009). This reduction essentially eliminated antlerless harvest as a significant factor in decreasing elk numbers and was expected to increase the survival of prime-age females, with their high reproductive value and recruitment of calves into the breeding population.

Cougar numbers were also managed by Montana Fish, Wildlife and Parks through hunts outside Yellowstone National Park. The Montana cougar hunting season was December through February during the years 1987–2000, was extended to December through April in winter 2000–2001, and continued during these months through the end of our study in 2006. Hunter-killed cougars were sexed and age-

estimated by the Montana Department of Fish, Wildlife and Parks Wildlife Laboratory (Aune and Schladweiler 1994). Fifty-five percent of the annual hunter harvest in these units during the period 1988–2005 occurred in the north portion of our study area and averaged 1.4 (range 0–2) adult females ( $\geq 3$  yrs old) and 0.6 (range 0–1) yearling/subadult females (1–2 yrs old) per year. During the same time span, annual hunter harvest averaged 1.8 (range 0–3) adult males ( $\geq 3$  yrs old) and 0.9 (range 0–1) yearling/subadult males (1–2 yrs old; Ruth et al. 2011). During our study wolves remained protected under the Endangered Species Act, which allowed no hunting of wolves (Bangs and Fritts 1996) except for lethal removal in cases of repeated depredation on livestock. Prior to publication of this book, wolves were delisted from endangered status, but they remain protected within Yellowstone National Park.

## SUMMARY

Our Northern Range study area covered approximately 3,779 km<sup>2</sup>, with roughly 57 percent in Yellowstone National Park and the remainder overlapping the adjacent Gallatin National Forest, Absaroka-Beartooth Wilderness, and private lands to the north of the park boundary. Elevations rise from about 1,500 meters along the Yellowstone River near Gardiner to more than 2,900 meters at the eastern end of the study area near where Soda Butte Creek and Slough Creek merge into the Lamar River, which then unites with the Yellowstone River. The Northern Range study area was accessible year-round by one paved road extending from

Gardiner to Cooke City, Montana. Thus most of our work was conducted on foot. The climate of the Northern Range consists of generally long, cold winters and short, cool summers.

Steeped in a history of volcanic activity, the productive Northern Range soils were derived largely from andesitic rocks, upon which grassland and sagebrush steppe predominate at lower elevations, with fir species and lodgepole pine at higher elevations. Fire is an important part of disturbance, vegetative succession, and patterns of forage availability in the Yellowstone ecosystem. Prior to wolf restoration, eight fires occurred. The most significant fire event took place when the 1988 fires burned more than 3,200 km<sup>2</sup>, including about 50 percent of forested areas in the park and 38 percent, or 1,451 km<sup>2</sup>, of our study area. Fewer fires occurred as we collected data on cougars after wolf restoration, with a total of nine fires burning roughly 344 km<sup>2</sup>, or 9 percent, of the study area. Herbivory by large and small mammals has a profound influence on the vegetation in Yellowstone National Park and surrounding lands. Numerically, elk outnumber all other ungulates and are more likely than other ungulates to influence vegetation, regulate ecosystem processes, and provide food for large carnivores. Most elk migrate from restricted low-elevation winter ranges to expansive high-elevation summer ranges located along hydrographic divides. While all animals were protected from hunting within Yellowstone National Park, ungulates and cougars were managed by Montana Fish, Wildlife and Parks through hunts outside Yellowstone National Park.

## CHAPTER 3

### Quantifying How Species Compete or Coexist

Competition, one of the major assumptions in Darwin's theory of evolution by natural selection, plays a role in natural selection because those individuals with traits that provide the best "fit" to local conditions tend to exclude and replace their weaker neighbors through rivalry and struggle for resources (Gause 1934; Hardin 1960; Caughley and Sinclair 1994; Begon et al. 1996; Keddy 2001: 41). This principle of competitive exclusion has become one of the fundamental tenets of ecology and forms the basis for studies of habitat partitioning and overlap as a way of measuring interspecific competition (Caughley and Sinclair 1994). Yet measuring how, when, and to what degree species compete and determining the influence of one species on another's population has remained difficult outside well-designed experiments, often laboratory experiments (Keddy 2001). Instead, tests for the effects of competition are commonly accomplished through indirect methods, relying heavily on inferences from patterns of niche overlap that support or contradict theories (Elton 1927; Wise 1984; Connor and Simberloff 1986).

In nature the larger *fundamental niche*, which provides the ecological conditions for a species to thrive in the absence of constraints, is rarely observed because the boundaries of *realized niches* are commonly set by competition with and predation from other species (Hutchinson 1959; Caughley and Sinclair 1994; Begon et al. 1996). It would be a very complex task to understand all the components of a species' niche. Fortunately, it is not necessary to make measurements along each and every niche dimension for the concept to be useful (Begon et al. 1996). For practical reasons the niche has come to be associated with use of certain resources, specifically sizes and types of prey, habitat, and space, and behavioral changes, such as activity or foraging

patterns (Schoener 1974; Caughley and Sinclair 1994). For our research we considered which main components of the niche were likely to provide advantages to cougars and wolves that would enhance their reproduction and survival, and thus population growth, and also which components were reasonable for us to measure on these large, elusive species. Given these constraints, we focused on three niche components of cougars and wolves: diet, spatial and habitat use, and temporal patterns of activity.

Patterns of overlap in diet or the types of habitat two species use or the way species forage provide weak inference of exploitation competition, underscoring the value of carefully designed field experiments where one species is reduced or increased in number and the response of the other species is then recorded (Caughley and Sinclair 1994; Krebs et al. 2001). Direct interactions between species provide a more concrete demonstration of the way species compete for a particular resource, but such direct interactions are difficult to document under natural conditions because, for example, they may occur quickly or at night, making them difficult to verify. The spatial scale, secretive behavior, and low densities of large carnivores make them less amenable to direct manipulation and experimental designs that provide for strong inference. In these situations the limitations of the field experiment make natural experiments, such as species introductions, attractive. Species introductions or removals have provided some of the strongest empirical evidence of population-level effects of interspecific interaction and competition (Connor and Simberloff 1986; Peterson 1995). In this chapter we present our study design and how we went about quantifying the food habits, spatial and habitat use, movements, and population characteristics of cougars and wolves.

## OUR STUDY DESIGN

Our study to examine competition and resource partitioning between cougars and wolves included four main components, following Keddy (2001).

### Changing Abundance of One Species

Wolf restoration set the stage for a natural additive experiment, and as numbers and distribution of wolves increased after restoration, changes in wolf abundance occurred naturally. With the restoration of wolves to the system, we asked whether increasing abundance of wolves would provide evidence of competition. This additive experiment was constrained in that we could only evaluate whether competition could potentially structure the community if densities increased to the level created during the natural experiment (Keddy 2001). We also acknowledged that resources might not be limiting enough during our study to see strong competitive effects between cougars and wolves, and competition probably would not affect all individuals equally.

### Incorporating Baseline Information or Controls

In natural field experiments individuals or populations that are not manipulated generally serve as controls or baselines. In our case, data on cougar population characteristics and predation prior to wolf presence (PW) served as our baseline for comparison to post-wolf restoration data (during wolf, DW). Because our studies occurred over more than a decade and at a large scale, we could not control the environment or how cougar and wolf populations responded to those changes. Thus, where we had available measurements to evaluate such changes, we incorporated temporal variation in the environment into our analyses.

### Measuring Resource Levels and Interference

Most resources are distributed in patches in space and time. Finding these patches and exploiting them is a fundamental challenge faced by all organisms (Keddy 2001). By measuring resource levels in both our baseline “control” (PW) and “treatment” (DW) study phases, we expected to determine where interactions occurred as well as which resources were potentially limited. Because high overlap in diet, habitat use, and spatial and temporal use may suggest the potential for competition, competitive interaction also required that we assess negative effects of wolves on cougars, including shifts in population trend or resource use patterns (Wiens

1989; Putman 1996). Conversely, we might document shifts in population trend or resource use, but these shifts should be causally related to and supported by comparative parameters of overlap and interference interaction.

### Measuring Population Performance

Ultimately, assessing competition between cougars and wolves is best addressed by gauging whether competition has effects on the fitness of individuals and impacts population performance in a negative manner (Keddy 2001). Thus we quantified survival, reproduction, and population growth of cougars before and after wolf presence.

While our study was grounded in these four components to quantify competition, as Keddy (2001: 185) observed, the various ways competition can play out emphasize that “one cannot divorce natural history from experiments, because careful observations of mechanism may yield some complex and unexpected methods of competition.” The time we spent following cougars day in and day out yielded important insights on how cougars made their living after the return of wolves.

## THEMES OUR RESEARCH ADDRESSED

*Interference and exploitation* competition between cougars and wolves might take several forms, which we have grouped into broad categories of food resources, landscape use by carnivores, and impacts to population growth, including direct killing of cougars (Creel et al. 2001; Caro and Stoner 2003; Mills 2007). In this section we provide a brief background to these larger themes guiding the organization of this book.

### Food Resources

When carnivores require similar food resources, the dominant competitor may be better able to exploit the patches of food. In avoiding the dominant competitor, the subordinate competitor might then switch to different types of prey or might forage in lower-quality food patches. For example, where African wild dogs and spotted hyenas coexist, wildebeest are the most important food item and are the second most preferred prey of African lions (Creel and Creel 1996). Greater abundances of spotted hyenas and lions translated into a reduction in the amount of food available for subordinate wild dogs.

Further, the dominant competitor may kleptoparasitize (steal food outright) from the subordinate competitor.



Kleptoparasitism is not uncommon in Africa, where spotted hyenas have been documented stealing food from 63 percent of lion kills in Chobe National Park, Botswana (Cooper 1991), and from upward of 86 percent of wild dog kills, as documented in five different studies (Caro and Stoner 2003). Frequent kleptoparasitism can increase the time costs and risks of hunting necessary to capture additional food lost to competitors, resulting in increased energy expended to obtain sufficient food (Gorman et al. 1998; Creel et al. 2001; Caro and Stoner 2003). For subordinate individuals, this might translate into increased rates of killing prey to compensate for food loss as well as into reduced reproduction and survival.

### Landscape Use

When the dominant competitor is better able to exploit patches of habitat that provide food, security, and denning, density of the dominant competitor may reach such a level that its use of certain limited habitats results in exclusion of the subordinate competitor from those areas. In turn, avoidance by a subordinate species might involve occupying different habitats, hunting at different times, or switching to different prey resources to minimize risk and perhaps provide an advantage over its competitor (Schoener 1974; Seidensticker 1976; Bothma et al. 1984; Durant 1998; Fedriana et al. 1999; Karanth and Sunquist 2000). In a heterogeneous environment, we might expect species with low competitive ability to seek out *competition refuges*, where competition is reduced (Durant 1998). In their study in Alberta, Fuller and Keith (1981) suggested that coyotes occupied the borders of wolf pack territories where wolves seldom ventured for fear of interpack encounters, and for coyotes such areas thus served as refuge from competition. As documented for cheetahs and wild dogs, subordinate species may survive best in areas with low prey abundance because areas rich in prey will be dominated by larger, more aggressive carnivores (Creel and Creel 1996; Durant 1998; Linnell and Strand 2000). So on the one hand, avoidance increases the odds of surviving by reducing the odds of mortality from direct encounters, while on the other hand, exclusion from rich foraging patches might reduce foraging efficiency for a subordinate species and thus indirectly reduce its reproduction and survival.

### Direct Killing and Population Growth

In addition to exploitation competition for food and habitat, as provided by some of the examples described, direct kill-

ing can also strongly influence population growth, depending on how frequently it occurs and what segments of the population—young, reproductive adults, or old—are most susceptible. Within the order Carnivora, interactions resulting in injury or death most commonly occur at kills (Creel et al. 2001). Such *intraguild predation* has been reported for at least ninety-seven pairs of carnivores involving fifty-four victim species and twenty-seven killer species, with annual mortality ranging from 4 percent to 76 percent (Palomares and Caro 1999). Among Carnivora, intraguild predators often do not eat their victims, so the killing is not predation in the normal sense. Depending on frequency of interactions, direct killing can result in a reduction in population growth of one or both competitors, although, again, effects are usually strongest for the subordinate species. One example comes from a study of cheetahs where mortality of kittens from birth to independence averaged 95 percent, of which 73 percent was a result of predation, mainly by African lions (Laurenson 1994). As hyena and lion densities increased, cheetah density declined (Caro 1994). When food becomes limiting, predators sometimes do feed on other carnivores. For instance, during a study in northern Canada, lynx were killed and eaten by wolves, wolverines, and coyotes when snowshoe hares became scarce (Krebs et al. 2001). Similarly, when hare numbers were low, lynx killed and ate red fox and other lynx, and great horned owls killed goshawks.

In aggregate, then, the intensity of competition depends on the degree of niche overlap, size and dominance of the competitors, and resource availability. Changing resource availability might cause shifts in the relative fortunes of the species concerned, but another tradeoff may also exist—a species may be a poor interference competitor yet be a better exploitative competitor, or vice versa (Holt and Polis 1997; Linnell and Strand 2000). Hence coexistence is also possible if the species more vulnerable to aggressive interactions and predation from a competitor is superior at exploiting certain resources; for example, cougars appear to be better exploiters of human-dominated landscapes than wolves are (Polis et al. 1989; Kortello 2005). Lastly, interference and exploitation competition can affect each other, such that strong interference competition could eventually weaken exploitation competition between the two species if cougar and wolf densities are reduced by one or the other, if the ratio of carnivores to prey decreases, or if cougars avoid wolves through shifts in space and habitat use (Polis et al. 1989).

These broad themes of competition translated into major themes in our research over time, and the research themes in turn gave rise to the main divisions in this book:

Part 2. Food Resources: Cougar-Wolf-Prey Relationships (including killing of carnivores)

Part 3. Landscape Use: Do Cougars Avoid Wolves?

Part 4. Before and after Wolf Restoration: Cougar Population Characteristics

The first chapter of each part presents the main working hypotheses and predictions for each topic addressed under that theme. Although we primarily tackle these topics relative to competition between cougars and wolves under the natural experiment of wolf restoration, we also attend to the role of bears in the competition equation. Information on how cougars and bears sorted out the landscape and the degree to which they interacted directly was necessarily more limited because no before-and-after experiment was possible, and not all grizzly bears and very few black bears were radio-marked in the study area.

In part 2, Food Resources, we cover competition for food resources, including direct interactions at kills. Here we describe the diets and prey selection patterns of cougars and wolves, analyze factors affecting kill rates of both carnivores and factors affecting detection of cougar kills by wolves and bears, and discuss the combined effects of cougar and wolf predation on prey. Examination of whether cougars partitioned habitat and avoided areas used by wolves is an aspect of part 3, Landscape Use. We explore how cougars used the landscape prior to and during wolf restoration, whether cougars made adjustments to increasing wolf densities by shifting home ranges away from wolf-dominated areas or by using different habitats, and if the area used by the cougar population as a whole remained constant. Part 4, Before and after Wolf Restoration, tackles cougar population characteristics and the question of whether wolf restoration substantially impacted cougar survival, reproduction, and population growth. In the synthesis in part 5, Carnivores and Humans, we integrate our findings and discuss them in relation to carnivore ecology as well as the conservation and management of carnivores in the Greater Yellowstone Ecosystem and beyond that to states that will be faced with management of cougars and wolves in the future.

## STUDYING COUGARS AND WOLVES

Determining population characteristics, rates of predation, and movement patterns presented various challenges to studying cougars and wolves. Documenting direct and indirect interactions between these carnivores took the challenges a step further. Cryptic coloration that blends in well with the surrounding vegetation and crepuscular and nocturnal activity are traits of cougars that did not lend to observing directly cougar behavior, predation, or interactions with other animals. Because they operate in packs, wolves were generally more visible and often observable from or near the road between Gardiner and Cooke City, Montana. Between February 2001 and November 2003, it was reported that at least one person, whether among park staff or visitors, had observed wolves in Yellowstone National Park every day, totaling at least 1,000 consecutive days of observation.

To obtain quantitative data that would answer questions regarding cougar and wolf ecology and interactions between the two species, we embarked on a rigorous effort to mark and radio-collar all individual cougars in the Greater Yellowstone Northern Range study area, both prior to and during wolf restoration. Following wolf restoration, the Yellowstone Wolf Project likewise continued to count wolves and, using radio-telemetry, to monitor all wolf packs that used the park (Smith and Bangs 2009). The Northern Range study area packs were most intensively studied to assess pack characteristics, movements, and rates of predation (Smith et al. 2001, 2004a, 2005). As a result, both our cougar studies and the wolf research benefited from a strong collaboration to monitor cougars and wolf packs across the Greater Yellowstone Northern Range (Ruth et al. 2003; Smith et al. 2005).

This section describes our general field methods of data collection, starting with how we determined the numbers of cougars residing within our study population and how we maintained contact with them through the radio collars we attached so we could collect the necessary data to understand population characteristics, predation, and habitat use and movement patterns across the study area. We collected data during all months of the year throughout the PW study from 1987 to 1994 and the DW restoration study from 1998 through March 2006, providing information over a total of almost fourteen years.

## MARKING COUGARS AND ESTIMATING POPULATION SIZE

To determine how many cougars used the study area during each winter, we combined efforts to mark and collar individual cougars with information from radio-telemetry locations of the increasing number of cats we marked, snow track transects, harvest reports north of Yellowstone, and sightings reported by Yellowstone employees and visitors (Murphy 1998). We estimated population size and density of cougars during winter by surveying for cougar tracks in snow while traversing non-overlapping transects. Field crews working on predation, non-invasive genetic sampling, and capture hiked and snowshoed approximately 1,500–1,700 km across various portions of the study area each winter during each study phase. While predation sequence crews recorded tracks as they located a focal individual, DNA and capture crews traversed 5 to 10 km transects on foot each day in a more systematic manner to cover the study area over ten to fourteen days. Avalanche danger, weather—such as temperatures of 25°C below zero or colder—and activity of multiple wolf packs in one area sometimes required that we remain out of the field or move elsewhere in the study area. During November to December and March of each winter, we also tried to avoid entering an area where wolves were under observation by Yellowstone Wolf Project personnel conducting kill rate sampling. Combined, our intensive efforts comprised 228 person-days of effort over five months of winter annually in the PW study and 226 person-days over four to five months of winter annually in the DW study.

Cougar and wolf tracks we encountered were entered on daily track investigation forms where we recorded the survey area, number of individuals, stride/straddle of the track pattern, snow tracking quality (STQ, following Halfpenny 1986), overall snow conditions (no fresh snow or categories of new snow measured in centimeters), and a Universal Transverse Mercator georeference of the track location. We used stride and straddle measurements, pad length and width, and toe size relative to pad size to classify cougar tracks as an adult male, adult female, subadult male or female, maternal female when tracks of kittens or yearlings were present with adult female tracks, or unknown sex/age.

Snow tracking data and all other sources of information regarding presence of radio-marked and unmarked cougars on the study area were compiled at the end of each winter to provide a minimum study population estimate. Unmarked

cougars were identified by comparing their movements and locations, determined by snow tracking or by direct observations, to those of radio-collared individuals (Murphy 1998: 82). We also followed up on sightings by residents and park personnel to estimate and potentially capture unmarked individuals and thus obtain a minimum estimate of cougars in the study areas each winter.

While our DW study was under way, non-invasive DNA sampling was growing in application as a method to identify and sex individuals; estimate abundance, distribution, and population growth rates; and examine patterns of genetic population structure of various carnivores (Woods et al. 1999; Ernest et al. 2000; Mowat and Paetkau 2002; Frantz et al. 2004; Long et al. 2008). Two DNA collection methods showed promise: hair snares and snow tracking (McDaniel et al. 2000; McKelvey et al. 2006; Ulizio et al. 2006). At the time no one had evaluated non-invasive genetic sampling methods for cougars against a known study population. As a consequence, we embarked on a collaborative project with cougar project technician and graduate student Mike Sawaya at Montana State University during three winters, 2003–5, to research the efficacy of non-invasive DNA sampling as a possible way to monitor cougar population trends in Yellowstone and other areas. These methods and results have been detailed by Sawaya and colleagues (2011), and results are summarized in chapter 14.

## Capturing and Radio-Collaring Cougars

During the PW study, 80 cougars were radio-collared and ear-tagged: 10 adult and subadult males, 14 adult and subadult females, and 56 kittens (Murphy 1998). After wolf restoration we radio-collared and ear-tagged 83 cougars: 19 adults (6 males and 13 females), 12 subadults (9 males and 3 females), and 52 kittens (28 males and 24 females). These numbers reflect designations into social classes at the time of capture. Some kittens and subadults later became established adults in the PW or DW study population. During the PW study an estimated 77 percent of adult cougars were radio-marked by winter 1988–89, with 87–94 percent radio-marked in all subsequent years until the final year of study. As wolves were restored, we radio-marked an estimated 68 percent and 88 percent of adult cougars present in the study area by winters 2000–2001 and 2001–2, respectively, with 88–93 percent radio-marked in all subsequent years until the final year of study (Ruth et al. 2011).



Our operations in Yellowstone National Park required capture protocols and special permits for the use of hounds and included yearly qualification with our Telinect® model dart gun. Each year we received hands-on training for avalanche and bear safety and attended animal capture and handling classes from five different veterinarians. General cougar capture and handling procedures followed Logan and colleagues (1986), Kreeger (1996), and Quigley (2000) and were approved by the Hornocker Wildlife Institute/Wildlife Conservation Society Animal Care and Use Committee, #1998-YCW-502, and by Yellowstone National Park officials under research permit #YELL-SCI-0039.

Throughout our capture season and all other times of the year, we accessed the study area by foot from the main paved road extending from Gardiner to Cooke City and from unpaved Forest Service roads and trails above Jardine, Montana, along the northern boundary of Yellowstone National Park. During the winter capture season, a team of three or four people carried in backpacks all collaring, telemetry, tree climbing, and medical gear necessary for capture while conducting tracking transects to search for cougar tracks and kills. So we could remain in the field for days at a time, we received special permission to use four National Park Service backcountry patrol cabins distributed along the central east-west axis of our study area (figs. 2.1, 3.1). Apart from a few special requests, we did not capture cougars in Yellowstone when bears were active outside dens, typically between March 15 and November 15 each year.

As we conducted track surveys, the houndsman or a researcher kept two to three hounds leashed and away from cougar tracks to minimize the time dogs were running free and might be detected and injured by wolves (fig. 3.2). This method also enabled our team to forward-track quietly without the hounds baying and pulling on leashes. We released hounds only on fresh cougar tracks or when we jumped a cat from a bed site or kill and only to capture new individuals or to place a new collar on an already marked individual. For ninety-nine captures using these procedures and where we recorded the time from when we released hounds to the time we arrived at the tree, we reached the treed cougar within a median of 20 minutes (average = 27 minutes, longest time = 183 minutes) and sometimes in as little as 30 seconds.

Once we arrived under the treed cougar, we immediately leashed the hounds and removed any stick or rock hazards



**FIGURE 3.1.** *Situated upriver from the Black Canyon of the Yellowstone River, Lower Blacktail cabin was one of four backcountry patrol cabins we stocked with food and other provisions. We received special permission to use these National Park Service backcountry patrol cabins, which enabled us to conduct fieldwork for extended periods of time. Photo by Toni Ruth, Hornocker Wildlife Institute.*

below the tree or buffered them with backpacks. Thus if a cougar did fall after darting, we minimized the potential for injury from objects on the ground. Treed cougars were initially darted with ketamine hydrochloride (Ketaset®) at a dose averaging 8.8 mg/kg (SD = 2.59, Ruth et al. 2010). Prior to wolf presence, Murphy (1998) used the Cap-Chur dart system. After wolf restoration, we used a Telinect dart system and shot 3 ml Telinect plastic darts (fig. 3.3). Once the cat was darted, the houndsman removed the dogs from the site and secured them far enough away for barking not to cause distress to the immobilized animal, while the remaining capture crew lowered the cougar safely to the ground (fig. 3.4). Once restrained on the ground, the cougar was sedated with 0.63 mg/kg (0.11) of xylazine hydrochloride (Rompun®) to reduce tension and provide analgesic properties.

The steep slopes (averaging  $30 \pm 15$  degrees) typical of the winter range often required that we move the cougar to a less steep area or to a more secure site on the slope, such as a natural depression upslope from a tree or rock. We usually located and prepared these sites prior to darting the cat (fig. 3.5). To provide for safe captures and to minimize capture-related complications (Kreeger 1996), we covered the eyes of immobilized cougars, examined them for any injuries, and monitored temperature, pulse, and respiration (normal



**FIGURE 3.2.** Awaiting our signal, Tony Knuchel keeps Cooter and Lark away from fresh cat tracks as we worked our way in to recapture and change the collar on adult female F125. Photo by Dan Stahler, Hornocker Wildlife Institute/Wildlife Conservation Society.

ranges: 37.8°–39.4°C, 60–80 beats per minute, 10–15 breaths per minute, respectively). We carried Dopram for respiratory arrest, epinephrine for cardiac arrest, Valium for seizures, two sizes of endotracheal tubes, suturing materials, betadine solutions, and other equipment necessary for emergencies related to lacerations or extreme changes in pulse or respiration rate. We also developed an emergency and euthanasia protocol as required by Yellowstone National Park and carried the euthanasia drug Euthasol® as well as potassium chloride (Kreeger 1996).

We encountered only two capture-related emergencies during fourteen years. In the PW study, a female kitten's tarsus was fractured by a misplaced capture dart. She was transported to a veterinary clinic, and following X-ray, her injury was repaired. After a period of rehabilitation, she was released and survived several years after her return to the

wild (K. Murphy, Yellowstone National Park, pers. comm., April 1998). During our wolf restoration study, an adult female cougar we captured under a shallow rock overhang had labored breathing, with breaths dropping to 5 to 6 per minute. We administered 0.55 mg/kg of Dopram followed with 0.06 mg/kg of the reversal drug Yohimbine to counteract the xylazine at approximately 30 minutes into the capture. Normal breathing resumed, and the cat became ambulatory within another half hour.

Ear tissue and blood samples for genetic analyses were placed in lysis buffer and stored at room temperature (Sawaya et al. 2011). Blood samples drawn for disease study were placed in heparinized blood tubes and, along with serum, were shipped to the National Genomic Laboratory, National Cancer Institute, Frederick, Maryland, or a lab at the University of Montana in Missoula for pathology and





**FIGURE 3.3.** Toni Ruth prepares to dart male M197 using a Telinject dart gun as Brad Shultz keeps his eye on where the dart hits. Photo by Polly Buotte, Hornocker Wildlife Institute/Wildlife Conservation Society.

genetics studies (see Murphy 1998; Culver 1999; Biek et al. 2006a, 2006b, 2006c, 2006d).

### Radio-Telemetry Collars

We used Very High Frequency (VHF) and Global Positioning System (GPS) radio-telemetry collars to track the movements and survival of individual cougars and wolf packs. Each VHF transmitter collar was affixed with a treated canvas expansion splice (yearlings and subadults), a durable seatbelt splice (resident adults), or an elastic expansion collar that we designed and affixed to Telonics MOD 125 and MOD 225 transmitters and placed on kittens age 10 weeks old or younger. With the help of project technician Craig Whitman, we improved on designs of Logan and Sweanor (2001) and Murphy (1998); we used non-twist elastic and sewed in three expansion seams so that collars would fit kitten neck circumferences of 18–31 centimeters but were

designed to expand to the average neck size of 34–42 cm for adult females or 44–53 cm for adult males without exposing the elastic, which could possibly wear into the neck. Although the elastic material could break through and make the collar drop within 12 months, we typically recaptured kittens at 4–6 months of age and placed on them a new, larger collar with a new expansion splice. Treated canvas expansion splices placed on yearling and subadult collars tore halfway through in 10.5–36 months, while other canvas splices rotted and completely broke away within 18–35 months (Ruth et al. 2010). One durable seatbelt splice used to fit a collar on an adult female rotted and broke within 5 years after she had eluded recapture. We removed most collars from adults through recapture or through the use of remote release mechanisms on GPS collars in the final year of our study.

In addition to VHF collars, our cougar project and the wolf project deployed GPS collars to help us achieve mul-



**FIGURE 3.4.** Jesse Newby secures a “Y-rope” and then a long climbing rope to the hind legs of immobilized subadult male M196 in preparation for crew members below the Douglas-fir tree to lower the cat safely to the ground. Photo by Tyler Coleman, Hornocker Wildlife Institute/Wildlife Conservation Society.

tiple project objectives that are discussed in later chapters, including kill rate sampling, simultaneous spatial and habitat use sampling with wolves, and movements of cougar subadults as they dispersed from the study area. Thus, between February 2001 and November 2006, we fitted a subsample of ten adult (five males, five females) and three subadult male cougars with GPS collars manufactured by Telonics® and Televilt®. Weight of GPS collars was 0.95–2.2 percent of cougar body mass (Ruth et al. 2010). As with VHF transmitter packages, we were concerned about the size of the transmitter box for collaring a hypercarnivorous species reliant on head mobility to kill prey. We placed Telonics store-on-board collars only on adult male cougars because of their larger neck size—average neck circumference 47.5 cm—whereas we placed other GPS collars on adult females,



**FIGURE 3.5.** After digging a trench in the snow, Erin Shanahan places a thermal blanket and insulating pad in preparation to radio-collar adult female F112 on the steep slope above the Black Canyon of the Yellowstone. Photo by Toni Ruth, Hornocker Wildlife Institute/Wildlife Conservation Society.

for which neck circumference averaged 38.9 cm, as well as on males (Ruth et al. 2010). We monitored GPS-collared cougars for periods that averaged 152.5 days (range = 9–329 days), for a total of 76 radio-months (Ruth et al. 2010).

### MONITORING COUGAR POPULATION CHARACTERISTICS: NEW ARRIVALS AND DEPARTURES

To assess population growth and demography, we monitored births and documented new immigrants and philopatry as additions to the study population. Departures from the population included deaths and emigration through dispersal of offspring born on the study area.



## Births

To determine litter size and sex ratio of litters and to estimate kitten survival and dispersal rate, cougar kittens less than 9 weeks of age were captured by hand at den sites detected by monitoring male-female associations, charting gestation periods of an average 92 days, and subsequently monitoring movement of females that supported newborns (fig. 3.6; Murphy 1998; Logan and Sweanor 2001). During the PW study, kittens were located in twenty-nine dens and marked at an average age of 4.5 weeks (range = 1 to 8 weeks) and at a mean age of 20.9 weeks (range = 10 to 52 weeks) of age after they had left the den (K. Murphy, unpubl. data). In the DW study, kittens were located in twenty-three dens and marked at the den at an average age of 5.6 weeks (range = 4.5 to 6.5 weeks) and at a mean age of 19.7 weeks (range = 9.5 to 54 weeks) of age after they had left the den. We radio-collared 57–78 percent of kittens in the PW study and 60–70 percent of kittens in the DW study prior to 3.5–4.8 months of age (Ruth et al. 2011). Those kittens we marked after they



**FIGURE 3.6.** Five-and-a-half-week-old male kitten M150 being measured and marked away from the den. Kittens were handled with gloved hands and returned to the den with their siblings after we had determined their gender and marked them. Photo by Toni Ruth, Hornocker Wildlife Institute/Wildlife Conservation Society.

had moved away from den areas with their mothers were captured and immobilized using the techniques for adults described earlier in this chapter.

## Deaths

To determine primary mortality factors and to estimate survival of adults, subadults, and kittens in our study area, we investigated sites of death and tried to ascertain the specific cause of all cougar mortalities. Each radio transmitter was equipped with a mortality sensor set to turn on after four hours of inactivity. Daily fieldwork conducted by field crews, combined with radio-telemetry location coordination with wolf project field crews, meant that we listened for signals of all radio-collared cats and wolves almost daily throughout the year. These procedures minimized delay in investigating mortality signals and increased the likelihood of determining cause of death or of recapturing cougars when collars dropped away or malfunctioned (Ruth et al. 2011). The Televilt Simplex and Tellus GPS collars provided us with a close approximation of time of death, as these collars recorded the first programmed location time associated with a signal switch to mortality mode.

After detecting a change in beats per minute, field personnel located the signal and hiked to the site to investigate. Snow cover, tracks and signs of struggle, hair, and other signs assisted us in determining cause of death. When we arrived at a site of death in a remote location, we performed field necropsies to look for hemorrhaging and other gross pathology that could yield clues to cause of death. When possible, we removed the cougar from the field and received necropsy assistance from veterinarian Dr. Kathy Quigley. Some cougars died for reasons that were obscure to us. In these instances, we collected organ and muscle tissues and sent them to the Wyoming Game and Fish Department Laboratory in Laramie for examination.

## Emigration, Philopatry, and Immigration

We monitored movements of dispersal-age subadults primarily through aerial telemetry flights, with flights ranging up to 200 kilometers from the primary study area. We documented distances traveled from the natal area and whether a disperser eventually established a home range or died. Because we did not always relocate dispersing individuals, we also garnered information for dispersal distance and fates of dispersers via hunter tag returns. Beyond these methods and in

hopes of gaining more detailed information on the day and night dispersal movements and habitat use of subadults, we placed GPS collars on three dispersal-age subadult males in the later years of our study. Data on dispersers were analyzed by field technician Jesse Newby for his master's thesis at the University of Montana (Newby 2011; Newby et al. 2013). In contrast to studies of dispersal movements where intense fragmentation constrained or frustrated dispersal of cougars (Beier 1995; Maehr et al. 2002), our efforts examined habitat preference of dispersers in a relatively intact landscape.

We estimated recruitment to our study population by counting philopatric offspring and cougars that originated elsewhere and then immigrated to establish residency on the Greater Yellowstone Northern Range study area (Logan and Sweanor 2001). At the beginning of each study phase, we were not always certain whether a young (28 to 42 months old) established cat was an immigrant or had been born on the study area. Yet within two years of our studies getting under way, we were able to identify newly captured, untagged cats within this age class as immigrants or philopatric cougars.

### THE WOLF POPULATION AND CAPTURES

Demographic parameters of wolves such as reproduction, survival and cause of death, density, and population growth rate were determined using observational and telemetry location data from both marked and unmarked individuals (Smith and Bangs 2009; Smith et al. 2009, 2010). All wolves released into Yellowstone were initially radio-collared (Bangs and Fritts 1996). The Yellowstone Wolf Project continued post-restoration capture and collaring efforts with the objectives of maintaining contact with each pack, keeping the breeders in each pack marked, and marking up to 50 percent of the pups born each year (Smith et al. 2009). Capture and handling of wolves was performed by the Yellowstone Wolf Project under the US Fish and Wildlife Service Endangered Species Permit #PRT-704930. Wolves were captured by darting or net-gunning from a helicopter during November to March each year (Smith et al. 2009).

The intensity of observations on wolves and the high proportion of marked animals in the population enabled the wolf project to enumerate population size reliably instead of relying on population estimators (Smith et al. 2009). Total pack counts were conducted in early and late winter, when each pack was observed over ten times per month during

two thirty-day periods of monitoring wolf predation. Annual reproduction was assessed by monitoring breeding females in each pack and subsequent observations of pups at dens and through the summer (Smith et al. 2009). The wolf denning season typically began in mid-April, when the breeding female localized around a den. Pack movements changed at this time, with wolves ranging in and out from this central den location. Mortality and survivorship of adult wolves was determined through radio tracking of collared individuals and field investigation within one week of receiving a mortality signal. Specific methods beyond these were presented by Smith and co-workers (2004a, 2009).

### PREY SELECTION AND PREDATION RATES

Cougar kills were documented by investigating potential kill sites located opportunistically during capture and population monitoring work, via predation sequence sampling on focal individuals, and by analyzing cougar feces following a method described by Murphy (1998). On Yellowstone's Northern Range, observations of wolves making kills and detection of wolf kills via ground and aerial observation were obtained most commonly during winter. Sampling of wolf kills during summer was less easily achievable and was not accomplished until after our study ended (see Metz et al. 2011). While we worked year-round to locate cougar kills, averaging about 40 to 50 kills in our cougar kill sample each year, the wolf kill sample accumulated at a rate averaging 68 to 190 kills documented each *winter* on the Northern Range (Smith et al. 2001, 2004a).

### Determining Gender, Age, and Condition of Prey

At kill sites we estimated percentage consumption of the carcass, recorded scavenger sign, identified species and gender of prey carcasses from skeletal or hair remains, and estimated an age class (young of year, yearling, or adult) using tooth replacement and wear patterns (Quimby and Gaab 1957; Robinette et al. 1957). When age or sex could not be determined during the PW study, Murphy (1998) used skeletal characteristics and made comparisons to known sex and age specimens for mule deer and elk (Denney 1965; T. Moore, Wyoming Game and Fish Dept., unpubl. data). When genitalia or skulls were absent from kill sites during the DW study, we determined the gender of prey remains via tissue sampling and gender polymerase chain reaction



amplification at the Wyoming Game and Fish Department Laboratory in Laramie (Anderson and Lindzey 2003; Ruth et al. 2010). This also enabled us to determine the gender of most elk calves. To determine cougar and wolf selection for different ages of prey in the DW study, we collected at least one of the first incisors (I1) from the lower jaw of ungulate prey greater than two years old. We submitted incisors to Mattson's Lab, Milltown, Montana, for aging by counting cementum annuli (Hamlin et al. 2000). For all DW kills, we estimated ages of ungulates using both cementum annuli and tooth wear patterns, except for some cases when incisors were not collected because part of the lower jaw had been chewed up or dispersed by a predator or scavengers. In these situations we estimated ages of ungulates using only tooth wear and replacement patterns, following the methods of Murphy (1998) during the PW cougar study (Quimby and Gaab 1957; Robinette et al. 1957). For elk, ages were estimated using tooth wear patterns specific to Yellowstone by using jaws of known-age elk as a reference. The question then became: Were our estimates of age by elk tooth wear a good predictor of age as determined from analysis of cementum annuli? We found a strong correlation between age estimated by tooth wear and cementum age (see notes at the back of the book for statistical detail), which allowed us to adjust estimated tooth wear age in months to cementum age equivalents for elk kills where we were unable to collect the first incisor [1].

We used femur bone marrow, one of the last stores of fat an animal uses, to ascertain physical condition of elk and deer (Cheatum 1949; Hornocker 1970; Mech and DelGuidice 1985; Husseman et al. 2003a, 2003b). Prior to wolf restoration, Murphy (1998) visually assessed femur marrow fat in the field. During the DW study, as an index to prey vulnerability, prey condition was estimated by analyzing femur marrow fat values in sections collected from kills (FMF = ratio of dry mass to wet mass; Neiland 1970; Kunkel et al. 1999; Husseman et al. 2003a, 2003b). Low marrow fat values indicated acute nutritional deprivation, although higher values did not negate waning condition (Mech and DelGuidice 1985; Harder and Kirkpatrick 1994; Cook et al. 2001). We also examined kills for abnormalities such as broken bones; calcification of metatarses, tibia, and ribs from previous breaks; parasites; and jaw necrosis.

Cougar and wolf kills were classified as possible, probable, or positive based on telemetric, sign, and pathological evi-

dence associated with each kill site (Murphy 1998); or the kill was classified as winter-killed, killed by another carnivore, or unknown. We used a categorization chart with increasing supporting evidence to categorize kills as possible, probable, or positive cougar or wolf kills, or as natural mortality (appendix A). Evidence that provided support of a probable or positive cougar kill included hemorrhaging or bites to the throat or base of the skull, no hemorrhaging or bites along the legs, caching or burial of the kill, and presence of bed sites (with cougar hair present) and toilets, which suggested that a cougar had spent enough time at the kill to eat and defecate (Beier et al. 1995; Bank and Franklin 1998; Ruth et al. 2010). Evidence that provided support of wolf kills was subcutaneous hemorrhaging indicative of injuries sustained before death along the posterior side of front and hind legs (areas grasped by wolves during prey capture) and signs of struggle and chase that included wolf tracks. Bears typically attacked the head and spine, whereas wolves attacked the flanks, hindquarters, and underside of the neck (Becker et al. 2009a). We used only probable and positive kills in analyses.

Weights of elk and deer were estimated using sex-specific growth models developed by Murphy (1998) and constructed from empirical data on live and field-dressed weights (Quimby and Johnson 1951; Greer and Howe 1964; Greer 1965; Robinette et al. 1973; Anderson et al. 1974; Pac et al. 1991; J. Mack, Yellowstone National Park, unpubl. data; D. Pac, Montana Fish, Wildlife and Parks, unpubl. data). We used these growth models to estimate the weight of killed prey when we knew the species, sex, age, and estimated date of death of the prey item. Weights of less frequently killed ungulate prey—bighorn sheep, pronghorn, mountain goat—were estimated from the literature (O'Gara 1978; Festa-Bianchet et al. 1996). We did not account for loss of carcass biomass to scavengers or how much of a carcass was consumed because these were highly variable, and we retained such kills in our analyses as we wanted to know what influenced variation in cougar kill rates (Ruth et al. 2010).

### Determining Kill Rates of Cougars

The sampling of focal individuals specifically to estimate cougar kill rates closely followed methods developed by Murphy (1998) during the PW study. We began by randomly selecting a VHF or GPS radio-collared cougar from one of five social classes—adult male, adult female, maternal female, subadult male, or subadult—for daily monitoring.



**FIGURE 3.7.** After using radio-telemetry to locate a cat, taking a compass bearing, and marking the site using a handheld GPS, Polly Buotte hangs a piece of flagging tape with the date and bearing written on it. These markers aided field personnel with searching sites where a cat had been located for kills on a later date, at which time the flagging was removed. Photo by Dan Stahler, Hornocker Wildlife Institute/Wildlife Conservation Society.

In the course of a VHF predation sampling sequence, our goal was to locate the focal cougar one to three times each day, search every prior location site, and continue the sequence until we documented more than two ungulate prey (elk, deer, bighorn sheep, antelope; Murphy 1998). Because access was limited to one road on our study area, we obtained all ground locations by hiking in an arc around the cougar to triangulate its location. We acquired at least three compass bearings and attempted at least two spaced at 90° without disturbing the individual or family group (fig. 3.7). We searched location sites by following compass bearings, determining a site center and error ( $= 33$  m,  $SD = 81$ ,  $n = 641$ ), and walking strip transects. These methods are described in

Ruth and colleagues (2010). On average we searched location sites within two days (range = 0–18) after cougars left the area. This intensive sampling methodology allowed us to calculate cougar predation rates in the presence of wolves and compare these to estimates of cougar predation rates from the PW study period.

When we carried out predation sequences on GPS-collared cougars in the DW period, we acquired locations from the collar through remote downloads. We plotted GPS locations in the geographic information system ArcInfo Version 8.0® and identified clusters of less than or equal to two GPS locations less than 200 meters apart as candidates for ground investigation (Anderson and Lindzey 2003; Mattson et al. 2007; Ruth et al. 2010). We located GPS cluster sites using a handheld GPS receiver (Garmin® etrex) and visited every location identified in the entire cluster, even if we found a kill at a previous GPS location. If we found no kill at cluster locations, we continued searching a larger area, as described in Ruth and colleagues (2010). Because location clusters may not form at some cougar kill locations, we evaluated whether we missed kills through cluster-only sampling and, if so, how many, by searching every GPS location ( $n = 392$ ) downloaded during three time frames on three individual cougars we located for a range of ten to forty-three days. We sampled 80 percent of the average estimated adult population during our PW and DW studies.

### Wolf Predation Monitoring

The Yellowstone Wolf Project searched for wolf kills by monitoring radio-marked wolf packs on the Greater Yellowstone Northern Range primarily during two winter periods each year—thirty days from mid-November to mid-December and thirty days in March (Smith et al. 2004a). Wolf packs were monitored and observed by ground crews and separately during flights. While aerial monitoring was dependent on weather, ground crews operated daily and tallied wolf kills independently from those documented by observers in the air (Smith et al. 2004a). Kills observed in between the two thirty-day predation periods—that is, between mid-December and March—were also documented by aerial and ground crews and included in prey selection analyses, but these data were not used in estimating wolf kill rates.

Wolf project field crews visited kills located by aerial and ground crews unless the kills were too remote from the road (Smith et al. 2004a). Kills were assigned species,

sex, and estimated age as noted by observers during flights, with accuracy of 84 percent. Because our studies coordinated data collection efforts as our cougar project got under way, when visiting a kill site in the field, wolf project crews collected data similar to what we have described for cougar kills.

## MOVEMENTS AND LANDSCAPE USE

To understand how cougars used the landscape before and after wolf restoration and how they interacted with wolves, and to test our hypotheses that cougars made spatial and habitat adjustments to wolf presence, we obtained daily to weekly locations of cougars through ground and aerial telemetry of VHF signals. We also downloaded locations from GPS store-on-board, pre-programmed, and query-on-demand systems. In addition to locations of VHF radio-collared wolves collected by the Yellowstone Wolf Project, we coordinated GPS location schedules with project leader Doug Smith to obtain a set of diurnal and nocturnal locations collected at simultaneous three-hour intervals on each carnivore species. Our programming of GPS collars changed during the study as different models of collars became available and were deployed (see Ruth et al. 2010). We first used Telonics® store-on-board collars programmed to attempt eight location fixes at 0100, 0700, 1400, 1600, 1800, 1900, 2100, and 2300 hours. After March 2003 we used only Televilt® brand collars and programmed them to attempt eight fixes at three-hour intervals between 0200 and 2300 hours.

Limited road access and the steep, rough topography of the study area meant that we could not obtain locations on cougars from roads or fixed stations. Consequently, we obtained all ground locations by hiking in an arc around the cougar to triangulate its location. We obtained at least three compass bearings and triangulated the location of the focal cougar without disturbing the individual or family group (Ruth et al. 2011). We located cougars from close proximity (generally 100–300 m) and used tree cover and topography and assessed direction of air currents to avoid disturbing cougars as we took at least three compass bearings. Prior to wolf restoration, cougars were located 6,560 times through triangulating on VHF signals from the ground and from airplanes. After wolf restoration, we located radio-collared cougars 5,373 times by triangulating on VHF signals with ground telemetry and locating VHF signals via fixed-wing aircraft. We also downloaded 19,531 locations from GPS collars.

We tested the accuracy of radio-telemetry locations by checking the areas for cougar sign, hidden test collars, dead cougars, and dropped collars. Our telemetry error averaged 33 m ( $SD = 81$ ) for 863 ground-based locations (Ruth et al. 2011). Mortalities and dropped collars that were located aerially and investigated by site searches from the ground had average aerial telemetry error of 161.7 m ( $SD = 216.0$ ,  $n = 41$ ) in the PW study and 156.8 m ( $SD = 121.1$ ,  $n = 21$ ) in the DW study.

We assessed habitat-induced bias on GPS collar fix success by placing four Televilt Tellus GPS collars in combinations of topography and canopy closure (Moen et al. 1996; D'Eon et al. 2002; D'Eon 2003; Frair et al. 2004; Hebblewhite et al. 2006). We sampled fifty-seven sites, stratified by three classes of canopy closure (less than 34 percent, 34–66 percent, and 67 percent and above) and five classes of available sky (less than 10 percent, 10–20 percent, 21–30 percent, 31–40 percent, and greater than 40 percent; D'Eon et al. 2002), for a total of fifteen site classifications with an average of three to four sites per classification. Available sky was a surrogate for topographic position where flat corresponded with 100 percent available sky, while a steep, narrow valley corresponded with a percentage of available sky obscured. We programmed the GPS collars to collect locations every three hours on the same time schedule as collars we deployed on cougars and scheduled an average of 56 relocation attempts (minimum of 15 and maximum of 156) per test site.

The average location fix success across all sites was 98 percent and ranged from 89 percent to 100 percent. Because habitat-related fix failures of less than 10 percent appear to have little effect on habitat selection results (D'Eon 2003; Frair et al. 2004), we did not correct for GPS bias in our habitat analyses. Despite our findings for high fix success across topographic and habitat types, GPS collars sometimes failed to obtain locations on cougars that likely corresponded with behavioral biases, such as cats bedding in dense vegetation and females denning under large complexes of boulders (fig. 3.8). However, we were successful at obtaining locations on denned females and on cougars resting in daybeds through VHF telemetry. VHF telemetry locations were limited primarily to daytime and biased toward resting and kill sites, although we occasionally followed and located traveling cougars during the day. In contrast, fix success rate of GPS collars was higher at night than during the day for most cats (fig. 3.9). While we could not correct for behavioral biases in

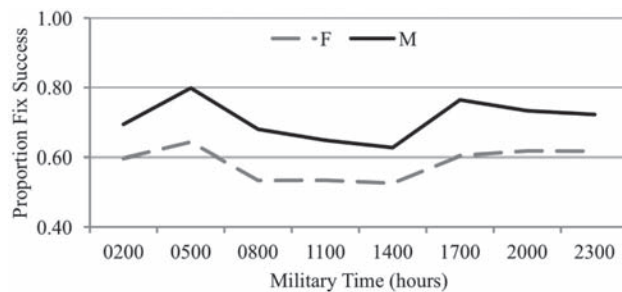




**FIGURE 3.8.** Cougars sometimes bedded, denned, and sought refuge from wolves and our capture attempts in large boulder fields in the study area. The cats had no problem bounding through this escape terrain, but for us, maneuvering through these boulder fields—particularly when they were snow-covered or wet from rain—was a slow, hazardous process. Subadult male M195 evaded our attempts to recapture him by disappearing into this extensive boulder field. Photo by Tyler Coleman, Hornocker Wildlife Institute/Wildlife Conservation Society.

our GPS location set, we used a combination of VHF and GPS locations in our analysis of cougar habitat use after wolf restoration, which could help to mitigate biases introduced by each method.

The Yellowstone Wolf Project located all radio-collared wolves through the year using fixed-wing aircraft and crews that obtained locations during ground fieldwork. Aerial locations averaged once per week for ten months of the year and almost daily during the two thirty-day study periods each year, mid-November to mid-December and in March (Smith et al. 2004a). As with all other aspects of our studies,



**FIGURE 3.9.** Fix success for ten female (F) and four male (M) cougars wearing GPS collars during the wolf restoration study phase on the Greater Yellowstone Northern Range, 2001–2006. Lower fix success during the day on cougars likely corresponded with behavioral biases, such as cats bedding and females denning under large boulders in our study area.

we assisted the wolf project with aerial and ground locations of wolves either opportunistically or upon request, and they reciprocated in assisting us to locate cougars. When wolves were seen, group size, activity, composition of the pack, and association with kills or den and rendezvous sites were recorded. GPS collars were placed on seven wolves in four packs that overlapped cougars on the study area and were programmed to attempt a location at the same time interval as GPS collars we placed on cougars.

## MONITORING NORTHERN YELLOWSTONE'S UNGULATES

Northern Range ungulates consisted of a mix of migratory and non-migratory groups, with elk and deer movements from summer to winter range influencing the seasonal movements and territory sizes of cougars and wolves (Murphy 1998; Smith and Bangs 2009; White et al. 2010). To quantify cougar selection of prey, assess competition for food between cougars and wolves, and incorporate prey numbers and movements in our analyses of cougar spatial-habitat use patterns, we relied on count and classification data from aerial surveys summarized by the Northern Yellowstone Cooperative Wildlife Working Group (Cross et al. 2009). In addition to these aerial surveys, the working group conducted spring carcass counts as a relative index to ungulate winterkill mortality. The group also monitored the results of the general and late-season hunts managed by Montana Fish, Wildlife and Parks. As the northern Yellowstone elk herd was one of the most studied elk populations in North America, we also tapped into the numerous research studies on elk mortality



and movements conducted during our PW and DW studies (Vore 1990; Coughenour 1994, Coughenour and Singer 1996a, 1996b; Mao et al. 2005; Evans et al. 2006; Barber-Meyer et al. 2008; and White et al. 2010 provide just a few examples).

### Elk and Mule Deer

Since 1986, annual trend counts of northern Yellowstone elk have occurred during December or January, and classification surveys have been conducted during February or March (Cross et al. 2009). The objectives of annual elk classification surveys were to: (1) classify a representative sample of the population, (2) estimate the overall sex and age (adult, juvenile) structure of the population, and (3) obtain an index of winter calf survival and recruitment via calf:cow ratio trends (Cross et al. 2009). No elk counts were conducted during the winters of 1996 or 1997, which coincided with years without cougar studies. Elk counts in 1989 and 1991 were deemed “poor” owing to unfavorable survey conditions (Cross et al. 2009). No classification estimates were obtained during the winters of 1993, 1994, or 1997.

Because landscape features and snow influence the sightability or detection of ungulates, raw counts substantially underestimated the actual abundance of elk, and the extent of undercount varied markedly among years, depending on survey conditions (Cross et al. 2009). Detection probabilities also likely changed between areas of the Northern Range following wolf recovery, with elk in the park more widely distributed in small groups and in timbered areas (Cross et al. 2009). We used information from three studies (Ackerman 1988; Pac et al. 1991; Eberhardt et al. 2007) to adjust elk and deer counts for sightability bias.

Spring surveys of mule deer on the Gardiner Basin winter range—Yankee Jim Canyon to Mammoth—were conducted between April 12 and May 17 each year beginning in 1986 (Cross et al. 2009). No surveys were flown in 1993 or 2004. Mule deer numbers were primarily stable during our studies.

### Bighorn Sheep, Pronghorn, and Mountain Goats

Prior to 1995, bighorn sheep populations in Yellowstone’s interior had not been surveyed from the air for almost fifteen years. Bighorns in the upper Yellowstone watershed do not typically display robust recruitment. Between 1992 and 1998, sheep recruitment north of Mammoth ranged from 6

to 32 lambs per 100 ewes (mean = 22 lambs/100 ewes; Cross et al. 2009), and following 1999, lamb recruitment was relatively high (range = 21–34; mean = 29 lambs/100 ewes). In late summer and early fall of 2000, “lamb pneumonia” mortality was documented north of Yellowstone National Park from LaDuke Springs south to Gardiner, Montana. In 2003 and 2004 Montana Fish, Wildlife and Parks administered the medication Fenbenazole to treat lungworm (Cross et al. 2009). Fecal analysis during the first year indicated that the medication had at least a short-term impact in reducing lungworm levels.

The Yellowstone pronghorn population was partially migratory, with a portion of the animals migrating 15 to 50 kilometers to four contiguous summering areas and a portion remaining year-round on the Gardiner Basin winter range (White et al. 2007). Spring pronghorn counts were conducted annually from 1988, with the exception of 1994. Late summer classification surveys were initiated in 1998, and counts of Yellowstone pronghorn have increased slowly and consistently since 1999, when 204 pronghorn were detected on the winter range (Cross et al. 2009).

Since the late 1980s, surveys have indicated that mountain goat numbers increased substantially in the Absaroka and Gallatin Mountains north of Yellowstone National Park and that goats expanded their range southward into the park. The status and distribution of mountain goats on the Northern Range was monitored in the southern portions of the Gallatin Range and Cooke City area and adjacent areas inside the park during September or October. Surveys by Montana Fish, Wildlife and Parks documented a two- to threefold increase after 1988 in mountain goats in two hunting districts adjacent to the north park boundary (Districts 323 and 329; Cross et al. 2009).

### Spring Carcass Counts

After 1989, elk and deer carcasses in the study area were counted annually from a helicopter in late April or early May. The aerial survey was used in conjunction with ground transect counts as a relative index of ungulate winterkill mortality, and these surveys were typically in agreement with regard to relative winterkill mortality (Green 1994; Podrutzny and Gunther 2006). An aerial carcass survey was not conducted in 1993, and only a partial count was conducted in 2004. During our studies two major winterkill events occurred during severe winters in 1988–89 and 1996–97, when hun-

dreds of carcasses were counted. We used carcass count data—carcasses per kilometer—when we assessed what factors influenced displacement of cougars from their kills by bears (see chapter 7; K. Gunther, Yellowstone National Park, unpubl. data, 2007).

## OVERVIEW OF STATISTICAL ANALYSES

We addressed the hypotheses and findings of our field research using the analytical and statistical techniques included in each of the relevant chapters. Additional details for certain of our analytical methods are given in the appendices. Statistical data and tests are referenced in the text by bracketed numbers (e.g., [1]) and are presented in notes at the back of the book.

We used non-parametric tests, such as Mann-Whitney *U* and Kruskal-Wallis tests, when the data did not meet assumptions of normality or equal variances or when sample sizes were small (Zar 1984; Gotelli and Ellison 2004). We transformed proportions and percentages with the arcsine square root transformation prior to using statistical tests (Gotelli and Ellison 2004). Most statistical tests and analyses were performed using MINITAB Statistical Software or the freeware R (R Development Core Team 2007). In chapter 15 we estimated survival rates of adults, subadults, and kittens and investigated the influence of various factors on survival using Program MARK and the known fate data type (White and Burnham 1999; Ruth et al. 2011; details of methods specific to our survival analyses are provided in Ruth et al. 2011).

Tests for differences between medians, means, and distributions are two-tailed unless otherwise specified. As is typical of studies of large carnivores, we were often dealing with small sample sizes. Therefore, we controlled for experimental errors at the  $\alpha = 0.10$  level of significance (Caro 1994; Logan and Sweanor 2001). The higher  $\alpha$  level reduces the probability of failing to reject a null hypothesis that is false (Type II error) and increases the probability of detecting a change. When exploratory tests for normality were rejected, we used non-parametric Mann-Whitney rank tests (Zar 1984). We report medians for non-parametric tests and provide means as additional descriptive information. For parametric tests, we report means and standard errors, unless stated otherwise, to express variability around the mean.

We used sets of a priori models to understand our system based on relationships specified within the model between explanatory variables and response variables, both of

which we measured. At times we investigated models that developed after initial analyses. We used output from these models to describe behavior of cougars in our study area, which in some instances might serve as a foundation for future work.

We used multiple linear regression, logistic regression, and multi-model inference to assess a number of characteristics in sets of a priori candidate models for prey selection, including characteristics of kill sites (chapter 5), predation rate (chapter 6), wolf and bear displacement (chapter 7), spatial and habitat use (chapters 10 and 11), and cougar survival (chapter 15; Hosmer and Lemeshow 2000; Burnham and Anderson 2002; Gotelli and Ellison 2004; Bolker 2008). We ranked models using Akaike's information criterion and the change in AIC values—either  $\Delta AIC$ ,  $\Delta AIC_c$ , or  $\Delta QAIC_c$  (Burnham and Anderson 2002). Where we report average beta and standard error estimates, these are calculated following Burnham and Anderson (2002) for each parameter in models within two AIC of the best model. For clearer presentation, we used model-averaged estimates for variables in the top models to calculate odds ratios and 95 percent confidence intervals when discussing our model results. The fit of logistic regression models to data was assessed with receiver operating characteristic (ROC) curves (Boyce et al. 2002). ROC curves are a plot of the fraction of observations coded with a 1 that were correctly classified as such versus the fraction of observations the model classified as a 1 but actually coded with a 0 that are obtained by varying the probability cutoff for classifying an observation as a 1. The area under the ROC curve (AUC) for a model with no predictive capacity (a straight line) would equal 0.5, while a perfect model would have an AUC of 1.0. Models with an AUC of 0.7–0.9 are considered to have useful application, and those with AUC values greater than 0.9 are considered highly accurate (Swets 1988; Manel et al. 2001).

## SUMMARY

Competition plays a role in the process of natural selection because those organisms with traits that provide the best fit to local conditions are able to out-compete their neighbors through rivalry and struggle for resources. Yet documenting competition is often difficult to achieve, with species introductions or removals providing some of the strongest empirical evidence of population-level effects of interspecific interaction. Wolf restoration provided a natural additive

experiment on the Greater Yellowstone Northern Range, enabling us to examine competition and resource partitioning between cougars and wolves with four main components to our research: (1) the changing abundance of one species between two time periods, (2) incorporating baseline information on cougars in the absence of wolves—that is, prior to wolf restoration, (3) measuring resource levels in both our baseline “control” (PW) and treatment (DW) study phases, and (4) measuring the effects on population performance before and after the arrival of wolves in the system. Interference and exploitation competition between cougars and wolves might take several forms, which we have grouped into broad categories of food resources, landscape use by carnivores, and impacts to population growth, including direct killing of cougars. These broad themes of competition translated into major themes in our research over time, and the research themes, in turn, gave rise to the central part divisions in this book.

To obtain quantitative data that would answer questions regarding cougar and wolf ecology and interactions

between the two species, we monitored an entire study population year after year. We accomplished this through winter snow track surveys and rigorous efforts to mark and radio-collar all individual cougars on the Greater Yellowstone Northern Range study area. During our PW and DW studies, a total of eighty and eighty-three cougars, respectively, were radio-collared and ear-tagged. We used VHF and GPS radio-telemetry collars to track the movements, kill rates, reproduction, and survival of individual cougars. We also used these technologies to understand how cougars used the landscape before and after wolf restoration and how cougars interacted with wolves, as well as to test our hypotheses that cougars made spatial and habitat adjustments during wolf presence. To quantify cougar selection of prey, assess competition for food between cougars and wolves, and incorporate prey numbers and movements in our analyses of cougar spatial-habitat use patterns, we relied on count and classification data from aerial surveys summarized by the Northern Yellowstone Cooperative Wildlife Working Group.





## **PART 2**

### **Food Resources**

#### *Cougar-Wolf-Prey Relationships*

Predation is exceedingly complex. On the one hand it involves the size of the predator population and the way in which predators capture their prey, including predator group size, choice of prey, and hunting methods. On the other hand, prey shows not only direct responses to a predator, such as flight, but also indirect ones which may be morphological, physiological, or behavioral. These manifest themselves in pelage color, birth season, herd size, and so forth—any responses that decrease the chance of a fatal encounter.

GEORGE SCHALLER,  
*THE SERENGETI LION* (1972: 195)





## CHAPTER 4

### Predation on the Greater Yellowstone Northern Range

Our knowledge of predator-prey relationships and the types of prey selected by cougars and wolves has advanced since the early 1970s. Yet much of this understanding comes from studies in systems where one of the large carnivores was present and the other absent (Hornocker 1970; Mech 1970; McClinton et al. 2000; Peterson and Ciucci 2003; Murphy and Ruth 2010). As elk hunting is economically and culturally important to the states that make up the Greater Yellowstone Ecosystem, wolf effects on elk have become a pinnacle issue in the region since wolves were restored (Smith and Bangs 2009). Effects of cougar predation fell into the background of public concern after the arrival of wolves, remaining of much lesser interest until recently. In contrast to single-prey systems, where only one type of large prey is present and carnivore diets are relatively simple, systems with multiple predators and multiple prey increase predators' options and the combined influence of predators on the various species of prey (Becker et al. 2009a).

Competition between carnivores for live prey as well as contests over dead prey have some bearing on how often each carnivore kills, affecting the ratio of predators to prey in the system and underscoring the complexity of predation in systems with diverse predators and prey (Polis and Holt 1992; Palomares and Caro 1999; Linnell and Strand 2000; Gunzburger and Travis 2005; Ruth and Murphy 2010b). Prey range in winter is limited in northern latitudes, and substantial overlap typically occurs between carnivore diets as the carnivores and ungulates congregate at lower elevations (Koehler and Hornocker 1991; Litvaitis 1992). Cougar and wolf reliance on similar prey could increase spatial overlap and the likelihood of interspecific aggression between the two carnivores. On the other hand, flexibility in prey choice by one carnivore may indicate that it is

a better exploitative competitor and may enable it to coexist with the more dominant competitor (Peterson 1995; Núñez et al. 2000; Maxit 2001). Even in light of similar prey choice, the abundance and distribution of food should also influence the extent of competition, with more abundant food potentially allowing for coexistence of carnivores. Where food abundance becomes limiting, interspecific interactions are predicted to increase, and the dominant competitor may exclude less aggressive species. Once the kill is made, carnivores may also compete by directly challenging each other for the carcass, and loss of kills to scavenging wolves (and bears) may force subordinate cougars to kill more often.

Before our study, little was known about cougar and wolf prey selection, predation rates, and competition for live and dead prey in systems with both carnivores present. Kunkel and colleagues (1999) discovered little separation in the sex, age, and condition of prey that cougars and wolves selected over four years in the relatively homogeneous forested landscape in and near Glacier National Park, Montana. During their three-year study in Idaho, Husseman and co-workers (2003b) found that cougars and wolves similarly preferred elk calves over other sex-age classes of prey, although elk in poor condition were more vulnerable to wolf predation. The data on cougar prey selection and kill rates accumulated by Murphy (1998) prior to wolf restoration made our study distinctively structured to assess not only whether cougars and wolves competed for similar prey but whether competition for live and dead prey actually altered prey selection and kill rates of cougars. This chapter sets the stage for those that follow on cougar and wolf prey selection, kill rates, interactions at kills, and the influence of these two carnivores on prey.

## HYPOTHESES AND PREDICTIONS

In chapter 5 we focus on cougar and wolf diets and prey selection and address these questions: Do cougars and wolves select similar prey species? Does dietary overlap then result in exploitative competition? Or is cougar prey selection driven first by prey abundance and vulnerability (size, naïveté, and condition) and not by competition with wolves until prey abundance and age-sex structure changes? Given that stalkers and coursers hunt in very different ways, are there factors that affect cougar and wolf prey selection and reduce dietary overlap? And, over time, do cougars switch to different types of prey to reduce competition from wolves?

In chapter 6 we look at the rate at which cougars and wolves kill prey. If wolves frequently detect and steal cougar-killed prey, do cougars kill more frequently than they did prior to wolf restoration? What factors most influenced the kill rate of cougars prior to and during wolf restoration? Our focus turns in chapter 7 to direct interactions at cougar kills. What factors influenced detection of cougar kills by wolves and bears? On average, how much biomass did cougars lose to competitors, and how much did competitors gain? Finally, we synthesize our findings and address the total annual effects of cougar and wolf predation on the Northern Range elk herd.

### Prey Selection

The degree of overlap in diet is the aspect most commonly examined to assess competition (Peterson 1995; Maehr 1997a). Among sympatric carnivores, prey species are often partitioned when body sizes or hunting styles of the carnivores are substantially different (Rosenzweig 1966; Gittleman 1989; Kunkel et al. 1999; Husseman et al. 2003b). Because cougars and wolves are similar in size, they may select similar prey species. Even so, vulnerability of prey to predation by each species of carnivore is a function of limits imposed by hunting style, the group or solitary behavior of the carnivore, and landscape features that enhance or detract from capture success.

Group hunting behavior, typical of wolves, should provide some advantages, such that much larger and more dangerous prey like bull elk or bison can be pursued and killed (Rosenzweig 1966; Gittleman 1989). But capture success of wolves tends to be low, and individual prey killed are commonly old, diseased, injured, or in poor nutritional condition (Mech 1970; Kunkel et al. 1999; Husseman et al.

2003b; Mech and Peterson 2003; Smith and Bangs 2009). In contrast, the stalking behavior of cougars suggests that they would have little opportunity to identify weaknesses and should favor random choice of individuals from a prey population (Rosenzweig 1966; Schaller 1972; Kleiman and Eisenberg 1973; Caro and Fitzgibbon 1992). Thus alternative hypotheses exist under which a predator might maximize hunting efficiency.

To maximize hunting efficiency, carnivores should respond to prey by occupying areas or patches of high prey density, thus maintaining a high rate of prey encounter and increasing successful capture rates (Taylor 1984; Bergman et al. 2006). This *prey-abundance* hypothesis predicts that cougars and wolves should prefer and make kills in areas where their primary prey are at the highest densities (Hopcraft et al. 2005). Yet vulnerability of prey may not be intrinsically linked to prey density—it may be defined by characteristics such as age, health, or features within the landscape that increase catchability of prey (Peterson and Ciucci 2003; Murphy and Ruth 2010). Further, the dichotomy in hunting techniques of cougars and wolves suggests that each carnivore should select prey that have different demographic or physical attributes (Kunkel et al. 1999; Husseman et al. 2003b). Under the *ambush-habitat* hypothesis, cougars should kill prey in habitats where prey are easier to catch or those with greater vegetation or topographically complex cover rather than in areas where prey densities are highest (Durant 1998; Hopcraft et al. 2005). The locations where wolves kill prey may be influenced more by prey attributes than by habitat characteristics—the *prey-attributes* hypothesis; yet encounters with groups of prey from which a coursing predator can select disadvantaged individuals should also be maximized under the prey-abundance hypothesis (Husseman et al. 2003b). If, in avoiding wolves, prey use more structurally complex habitat, thus increasing their risk of predation from cougars, then cougars may benefit via *predation facilitation* (Charnov et al. 1976; Kunkel 1997; Losey and Denno 1998, 1999; Atwood et al. 2009). In combination, cougar and wolf predation may offset influences on particular prey species or sex-age classes of prey, or the cougars and wolves may act synergistically in an additive manner and have stronger influences, resulting in the complex of predator species killing more prey in combination than their individual impacts would be where one carnivore exists in the absence of the other (Soluk 1993).



Following from these hypotheses, we made these predictions:

1. If elk remained abundant during our study, cougars and wolves should select similar prey types, and cougar selection of prey should be similar to prey selection prior to wolf presence. High dietary overlap would provide evidence of exploitative competition between the two carnivores.
2. Over time, dietary composition of cougars and wolves might diverge as wolf populations become established and prey abundance becomes limited, providing further evidence that exploitative interactions occurred between the two species (Wiens 1993; Kortello et al. 2007). In this scenario we expected that cougar diets might shift to alternate prey species to reduce competition, and diets of cougars should then also differ from their PW diets.
3. Although cougars and wolves select similar prey species, wolves should kill a greater proportion of young, old, and nutritionally compromised prey relative to cougars, as these prey are easier to select out of a group of running elk with wolves in hot pursuit.
4. Wolves should also kill prey in areas of less cover and on lower slopes that facilitate their coursing hunting behavior compared to forested, rough terrain where cougars optimally stalk and kill prey. While the first three predicted differences in prey selection would not be expected to reduce exploitation competition significantly, differences in habitats where prey are optimally killed by the two carnivores should reduce interference competition. In avoiding wolves, we predicted that cougars should now make more kills in forested or topographically complex habitat, perhaps in areas used less by prey, than their PW counterparts did because such areas enable catchability of prey while also enhancing concealment, thus reducing risk of detection from competitors.

### Kill Rates

Wolves either killing cougars or appropriating their food resources by directly displacing them—or vice versa—provide evidence of interference competition (Case and Gilpin 1974; Murphy et al. 1998; Ruth 2004a; Kortello et al. 2007). Although use of cougar kills by dominant competitors has been increasingly documented, whether cougars compensate for losses by killing additional prey, thus increasing their kill rate to offset energetic costs, is not well documented

(but see Harrison 1990; Murphy et al. 1998). We hypothesized that wolves would compete directly for carcasses of prey killed by cougars. If subordinate cougars are frequently displaced from kills by dominant competitors, they should need to kill again more quickly than if they were not disturbed. Greater spatial overlap of cougars and wolves during winter might also positively influence detection of cougar-killed prey. Thus with the return of wolves to the Greater Yellowstone Northern Range, we made these predictions:

1. Cougar kill rates should increase from PW kill rates if wolves, in conjunction with bears, frequently located and displaced cougars from their kills. First, we predicted that kill rates of cougars within specific social classes should increase as a result of kleptoparasitism by wolves and bears. We expected that competition for carcasses would most greatly affect maternal female cougars because, to support offspring, they make kills frequently—about one kill every six to seven days—thus providing more carcasses on the landscape that might be detected by competitors (Murphy 1998). Hence we further predicted a significant increase in predation rate within the maternal female social class and less of an effect on other cougar social classes. Because we expected maternal female cougars to be displaced from kills most frequently, we also predicted the resulting annual number of prey killed by certain social classes to be higher than they would otherwise have been. Alternatively, if elk remain abundant, cougars and wolves might rarely interact at kills because of wolves' high rates of encounter with abundant prey.
2. Extra costs of thermoregulation during cold weather, functional predatory responses to increased densities of prey on winter range, and declining condition of prey might influence how frequently cougars kill—generally resulting in increased kill rates of cougars during winter compared to summer (Fuller 1991; Murphy 1998; Mech et al. 2001; R. C. Cook et al. 2004; Becker et al. 2009a, 2009b). Because greater overlap with wolves during winter months might subject cougars to increased displacement from kills, we predicted that DW cougars should: (1) kill at higher winter than summer rates and (2) have higher winter kill rates than those of their PW counterparts. In contrast, cougars have shown higher kill rates in spring and summer as related to the ungulate birth pulse, which produces an increased density of small, naive prey that are easy to encounter and

kill (Mattson et al. 2007 in Arizona; Knopff et al. 2010b in British Columbia, Canada). Hence the functional response by predators should result in a higher frequency of killing in spring-summer, and we explored this hypothesis as well (Holling 1959).

3. Differences between cougar kill rates prior to and during wolf restoration should be greatest during winter months and be positively related to the number of displacements by wolves. Alternatively, wolves may enhance cougar access to elk (predation facilitation) by changing elk distribution (calving and foraging areas) to more closed and rocky habitats, thus facilitating cougar predation on elk. Thus cougar kill rates could similarly increase from PW kill rates as a result of predation facilitation by wolves.
4. A reduction in cougar kill rates would be suggestive of cougars having to travel farther and spend more time searching for lower-density prey. If this occurred, we predicted that cougars should spend a similar amount of time feeding at, or handling, kills and spend longer times traveling and hunting between kills compared to their PW counterparts. Further, if dominant wolves gained significant benefits from frequent feeding on cougar-killed prey, we would also anticipate an offset in the wolf kill rate.

### Interactions at Kills

Wolves, coyotes, grizzlies, and black bears scavenge from cougar kills and occasionally displace the cougar (Murphy et al. 1998; Ruth 2004a, 2004c). Such direct interactions typically favor wolves because wolf group sizes are larger than those of cougars and because cougars appear more cautious in defending their kills (Koehler and Hornocker 1991; Murphy 1998). Loss of kills to scavenging wolves (and bears) may result in increased energy expenditure per cougar kill, a decreased interval between kills, and thus an increased rate of predation by cougars to compensate for loss of food and to meet daily energy requirements.

At the outset of our post-wolf restoration study, we hypothesized that wolves would be frequent and dominant visitors at cougar kills, particularly during winter, when cougars and wolves typically overlap more extensively on ungulate winter range and wolf encounter rates with cougar kills could be greater (Ruth 2004a; Ruth and Murphy 2010b). We also expected that bears would visit and displace cougars from kills during spring, summer, and fall at a frequency similar to or lower than during the PW period.

We hypothesized that interference competition from wolves at cougar kills should be influenced by wolf density and use, landscape features, and prey size. Interference competition from bears should be influenced by time of the year (seasonal), landscape features, prey size, and the availability of other foods—pine nuts, berries, and winter-kill—during the year. Our predictions, to be detailed more fully in table 5.1, were:

1. The odds of a cougar being displaced by wolves should be greater for large ungulate prey, in open cover types, with higher wolf use, on gradual slopes, and during winter.
2. The odds of a cougar being displaced by a bear should decrease with increasing availability of other carcasses and should be higher for carcasses of large prey, in open areas, on gradual slopes, and during spring.
3. Cougars displaced from kills by wolves and bears should make another kill more quickly than when they were not disturbed from feeding. We predicted that a lower frequency of visits by bears to cougar kills could occur if bears were more likely to detect and encounter wolf-killed prey.

### Combined Influence of Cougars and Wolves on Elk

In the final chapter of part 2, we synthesize our findings from chapters 5 through 7 and examine whether predation by cougars was a strong top-down force adding to that of wolf predation to limit growth of the elk population. We evaluate these hypotheses:

1. Exploitation competition among cougars, wolves, and bears would result in an increased proportion of elk calves removed annually in the DW period compared to the PW period. As a result, a proportion of cougar predation would be additive to that of other carnivores, such that the recruitment of elk calves would decline.
2. An increasing ratio of carnivores to elk, increased offtake of elk calves by carnivores, and sustained hunter harvest of prime-age cow elk would be additive top-down forces strongly limiting growth of the elk population.
3. The annual total predation rate of cougars would become inversely density-dependent, or depensatory, as the elk population declined and cougars killed a larger proportion of the elk population. When the total predation rate of cougars is added to that of wolves, the depensatory relationship should increase in strength because both predators acquire a larger proportion of the elk population.

## CHAPTER 5

### Prey Selection by Cougars and Wolves

#### CONTRIBUTING AUTHORS

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Most obvious in the equation of which prey types cougars and wolves might similarly select and for which they may thus compete is the abundance of one prey species relative to other prey. Yet an elk or mule deer might be encountered more often or less often than would be predicted by its abundance because of the influence of habitat types, selective searching by predators and their decisions to hunt, or active avoidance of predators by prey, including the formation of groups (Mech 1977a; Greene 1986; Huggard 1993; Creel and Creel 2002). The vulnerability of prey is also mediated by their size, age, experience, and nutritional condition as well as by abiotic factors including snow depth and crusting (Errington 1946; Greene 1986; Quinn and Cresswell 2004; Hopcraft et al. 2005; Murphy and Ruth 2010). Similar to various attributes of prey, the age, gender, experience, reproductive status, past success, and individual preferences of carnivores work in concert to influence their selection of prey (Peterson and Ciucci 2003; Murphy and Ruth 2010).

In this chapter we contrast prey selection by cougars and wolves in four primary ways to test hypotheses and predictions laid out in chapter 4. First, we examine whether cougars selected different species and sex-age classes of prey as wolves colonized the study area compared to their pre-wolf counterparts and to what extent elk fall prey to cougars and wolves because of small size and naïveté when young or because of old age. We do so by comparing the abundance of prey types and the sex-age composition of prey to the proportion of kills made by cougars and wolves. Second, we assess whether cougars selected elk in similar nutritional condition and of similar ages to elk that wolves selected. Third, we evaluate whether cougars switched to alternate, less abundant types of prey or to different age classes of prey in this multiple-prey system. Finally, we assess the influence

of habitat and scale of hunting to address the prediction that habitat structure influenced prey vulnerability to cougars, whereas risk of predation by wolves should be influenced more by attributes of the prey (e.g., size, condition; Kunkel et al. 1999; Husseman et al. 2003b; Bergman et al. 2006).

#### DOCUMENTING THE DIET OF COUGARS AND WOLVES

Once we discovered a prey carcass, we conducted a field necropsy to determine whether a cougar, wolf, or bear had made the kill or if the animal had died of natural causes. This involved searching for tracks, carnivore hair, and presence of scats and evaluating patterns of injury to the prey and presence or absence of prey caching by the predator (O’Gara 1978; Kunkel et al. 1999). In chapter 3 and appendix A we describe our methods of documenting kills, as well as how we classified kills, in greater detail. Because our fieldwork was focused on cougars, 98 percent of the carnivore kills we located were made by cougars. Yellowstone Wolf Project personnel were similarly focused on finding kills made by wolves and used a similar system of classification.

As a result of our combined field efforts, Murphy’s (1998) PW and our DW restoration study documented 312 and 465 cougar-killed prey, respectively. In table 5.1 we provide the proportion of all prey in the diet of cougars prior to and during wolf restoration. Cougars killed individuals of fourteen species of non-ungulate prey, including other cougars, which were sometimes partially consumed (table 5.2). When prey species other than ungulates were excluded from our kill sample, 252 kills in the PW study and 432 kills in the DW study represented large ungulate prey. Elk remained the most abundant prey and the staple year-round food of cougars over fourteen years of research, although their numbers

declined between 2001 and 2006 (Murphy 1998; Smith and Bangs 2009). Elk represented 60 percent of the PW sample and 74 percent of the DW sample (see also fig. 5.1). Mule deer were the second most important ungulate prey in the cougar diet, making up 23 percent and 15 percent of the cougar diet prior to and during wolf restoration, respectively. Cougars preyed on other ungulates to a much lesser extent—bighorn sheep (less than 3 percent in both studies), pronghorn (2.3 percent DW), and moose (1 percent PW); we discuss this in more detail later in this chapter.

Wolves also favored elk over other prey. Elk made up 84 percent and 95 percent of wolf kills during March–April 1997 and November–December 1997, respectively (Smith et al. 1989). Over the remainder of the study, wolves focused

**TABLE 5.1.** Number and proportion of ungulate and small prey in the diet of cougars prior to (1987–94) and during wolf restoration (1998–2005) on the Greater Yellowstone Northern Range, Montana and Wyoming.

| Prey Species   | Sex–Age Class | Pre-Wolf |      | During Wolf |      |
|----------------|---------------|----------|------|-------------|------|
|                |               | Total    | %    | Total       | %    |
| Elk            | Calves        | 124      |      | 181         |      |
|                | Cows          | 41       |      | 124         |      |
|                | Bulls         | 16       |      | 30          |      |
|                | Unknown       | 7        |      | 10          |      |
|                | Total         | 188      | 60.3 | 345         | 74.2 |
| Mule deer      | Fawns         | 22       |      | 22          |      |
|                | Does          | 18       |      | 20          |      |
|                | Bucks         | 15       |      | 13          |      |
|                | Unknown       | 2        |      | 9           |      |
|                | Total         | 57       | 18.3 | 64          | 13.8 |
| Bighorn        | Rams          | 1        |      | 6           |      |
|                | Ewes          | 2        |      | 6           |      |
|                | Total         | 3        | 1.0  | 12          | 2.6  |
| Pronghorn      | Adults        | 1        |      | 7           |      |
|                | Fawns         |          |      | 2           |      |
|                | Unknown       |          |      | 1           |      |
|                | Total         | 1        | 0.3  | 10          | 2.2  |
| Moose          | Adults        |          |      |             |      |
|                | Calves        | 3        |      |             |      |
|                | Total         | 3        | 1.0  | 0           | 0.0  |
| Mountain goat  |               | 0        | 0.0  | 1           | 0.2  |
| Other prey     |               | 60       | 19.2 | 33          | 7.1  |
| Total all prey |               | 312      |      | 465         |      |

**TABLE 5.2.** Numbers and species of non-ungulate prey killed by cougars and wolves on the Greater Yellowstone Northern Range, 1987–2005.

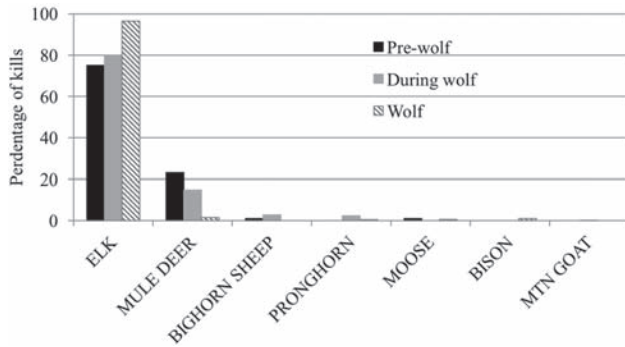
| Prey Species      | Pre-Wolf<br>Cougars | During Wolf<br>Cougars | Wolves |
|-------------------|---------------------|------------------------|--------|
| Cougar            | 15                  | 8                      | 7      |
| Wolf              |                     |                        | 14     |
| Coyote            | 12                  | 10                     | 23     |
| Red fox           |                     | 1                      |        |
| Badger            |                     |                        | 2      |
| Marmot            | 5                   | 7                      |        |
| Porcupine         | 19                  | 5                      |        |
| Snowshoe hare     | 4                   |                        |        |
| Cottontail rabbit | 1                   |                        |        |
| Red squirrel      | 1                   |                        |        |
| Chipmunk          |                     | 1                      |        |
| Mouse             | 1                   |                        |        |
| Sandhill crane    |                     |                        | 1      |
| Blue grouse       | 1                   | 1                      |        |
| Golden eagle      |                     | 1                      | 1      |
| Saw-whet owl      | 1                   |                        |        |
| Short-eared owl   |                     |                        | 1      |
| Raven             |                     |                        | 1      |
| Unknown           |                     | 2                      | 71     |
| Total             | 60                  | 36                     | 121    |

on elk slightly more than did cougars, with elk making up 97 percent of the 1,450 documented winter and summer kills for the period 1998–2005 (fig. 5.1). Mule deer, pronghorn, moose, and bison each made up 1 percent or less of the wolf diet. Wolves also killed at least nine species of non-ungulate prey, including other wolves, which were sometimes fed upon (table 5.2).

## SELECTION OF PREY

To test for nonrandom prey selection, we used annual counts of prey from aerial surveys conducted by the Northern Yellowstone Cooperative Wildlife Working Group (Lemke et al. 1998; Taper and Gogan 2002; Smith et al. 2004; White et al. 2008; Cross et al. 2009). A problem with the count data was that aerial surveys undercounted species of interest because of some proportion of animals being less visible to observers during flights (Caughley 1974; Samuel et al. 1987). Consequently, we adjusted all elk counts upward using the “raising factor” of 1.32 from Eberhardt and colleagues (2007)





**FIGURE 5.1.** Proportion of ungulates killed by cougars prior to wolf restoration ( $n = 252$ ) and during wolf restoration ( $n = 432$ ) and of ungulates killed by wolves ( $n = 1,529$ ) on the Greater Yellowstone Northern Range, 1987–2005.

and adjusted mule deer counts upward using the raising factor of 1.59 (Pac et al. 1991; Murphy 1998). In March of each year, counts were conducted by helicopter to classify approximately 20 percent to 30 percent of the northern Yellowstone elk herd into sex and age classes of calves, cows, and bulls (Taper and Gogan 2002; Smith et al. 2004; Cross et al. 2009). We used these data to compare the proportion of sex-age classes of elk and deer killed by cougars to prey killed by wolves. We also used these data to determine selection of prey by each predator (Begon et al. 1996; Estes et al. 2003).

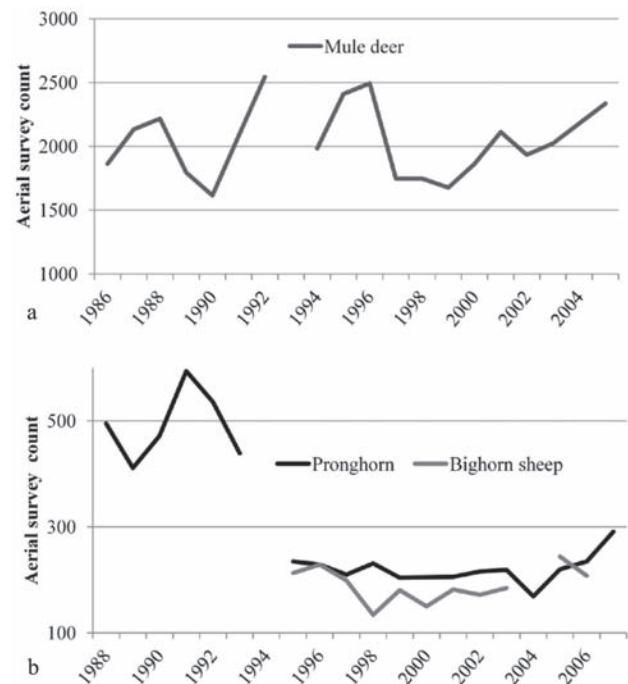
While recognizing that individual cougars and wolf packs select prey from those available within their home range or territory, in the DW study we were primarily interested in population-level comparisons of cougar and wolf predation over time, such as prey selection by cougars prior to and during wolf restoration and across the years of each study period. Similar to Murphy (1998), we found that adult female, adult male, and maternal female cougars did not kill different proportions of large versus small ungulate prey in either study phase [1].

Although age and condition play a role in ungulates' vulnerability to predators, both are also linked to pregnancy rates of ungulates. Failure of cow elk to breed on the Greater Yellowstone Northern Range was a function of their fat levels (Cook et al. 2001). Compared to the low reproductive value of calves, which did not contribute to the population until their second year, cows that were 1–14 years of age had high survival and high pregnancy rates on the Northern Range (Cook et al. 2001; R. C. Cook et al. 2004). The reproductive

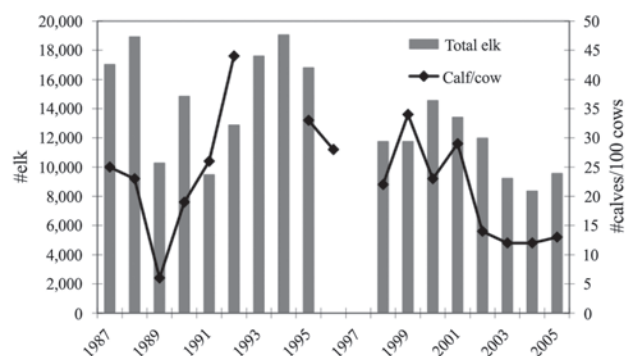
value of cows older than fourteen years declined steadily, primarily because of declining body condition (R. C. Cook et al. 2004). Following the pregnancy rate age categories provided by Cook and colleagues (2001), we used cementum age and the cementum age equivalent adjustment described in chapter 3 to classify elk kills into categories of calves (0 to 12 months), prime adults (greater than 12 months but less than 15 years), and old adults ( $\geq 15$ ) for our comparison of cougar and wolf prey selection.

### Prey Abundance and Trends

Throughout the study, elk were numerically more abundant than mule deer, pronghorn, and bighorn sheep combined by an average ratio of four to eight elk to each of these other ungulates (see fig 5.2). On average, elk constituted 88 percent to 94 percent of the total biomass of elk, mule deer, pronghorn, and bighorn sheep prior to and during wolf restoration. Although the abundance of calves, cows, and bulls in the elk population varied across the years of each study



**FIGURE 5.2.** Aerial survey counts of mule deer (a), pronghorn, and bighorn sheep (b) on the Greater Yellowstone Northern Range, conducted by the Northern Yellowstone Cooperative Wildlife Working Group, 1988–2007.



**FIGURE 5.3.** Minimum number of elk and calf:cow ratio trend for the Northern Range elk herd, 1987–2005. Note the decline in calf:cow ratio in 2002.

phase, cows made up the bulk of the elk population. In the PW study, cow elk ranged from a high of 83 percent in 1989 to a low of 53 percent in 1995. The proportion of calves in the elk population declined from 16.1 percent following the fires of 1988 to 5 percent in 1989 and rebounded to a high of 27 percent by 1992 (fig. 5.3). In the DW study, cows ranged from a minimum of 53 percent of the available elk population in 2001 up to 75 percent in 2005. Calves declined noticeably, from 18 percent of the available elk in 1999 to 9 percent in 2004. Bull elk made up from 11 percent to 23 percent of the elk population in the PW period, reached a maximum of 31.8 percent during early wolf restoration, and declined after 2001. By 2005 bulls made up 15.3 percent of the available elk population. Mule deer abundance remained mostly stable over the PW and DW study periods (fig. 5.2a; Lemke 2005; Cross et al. 2009).

### Cougar Prey Selection before and during Wolf Presence

Prior to the restoration of wolves, cougars killed elk less often than expected based on elk abundance, and they killed mule deer more often than expected (Murphy 1998). As wolves became established, cougars killed elk and mule deer in proportion to their abundance, whereas wolves killed elk more often and mule deer less often than expected based on their availability across the study area [2].

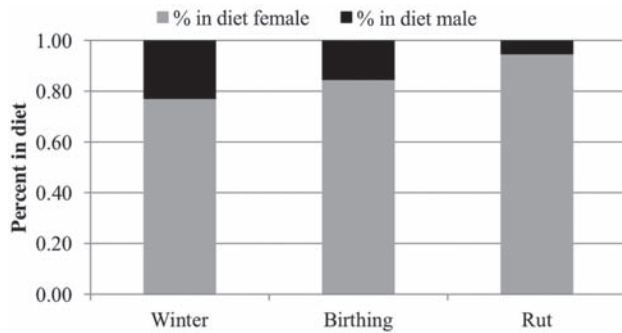
Elk calves were the most important prey for cougars relative to their abundance during both the PW and DW study periods (Murphy 1998) [3]. During both study phases

cougars selected adult elk (cows and bulls combined) substantially less than their abundance on the Northern Range. Prior to wolf restoration, cougars selected mule deer fawns, does, and bucks next, relative to their abundance; but after wolf restoration cougars selected fawns, does, and bucks in proportion to their abundance. Because efforts to examine cougar predation north of the Yellowstone Park boundary were more extensive during Murphy's (1998) PW study, and this could explain the PW/DW differences in the proportion of mule deer in kill samples, we removed deer and only considered elk. This revealed that in the DW study, elk calves made up a lesser proportion and adult elk a greater proportion of the cougar kill sample than in the PW study [4].

Prior to wolf restoration, Murphy (1998) concluded that large ungulate prey appeared less vulnerable to cougar predation during reproductive periods than during winter. After wolf restoration, we examined the hypothesis that vulnerability of adult ungulates should increase during reproductive periods compared to non-birth and non-rut periods. We did not find support for reproductive vulnerability of adult female and male elk, which contrasted with findings for cougars in a system where deer were primary prey in Alberta, Canada, by Knopff and colleagues (2010b). Instead, bull elk made up a greater proportion of the cougar diet in winter, indicating a lack of support for the hypothesis that male elk were more vulnerable during the rut, although post-rut condition of bulls was likely affected by winter vulnerability (fig. 5.4) [5]. Female elk also did not have a greater chance of being killed during calving than in winter. While the vulnerability of smaller ungulates such as deer, pronghorn, and bighorn sheep may increase during birth and rut periods, large ungulate prey in our system appeared to be less vulnerable during reproductive periods. As winter progressed from January through May, adult elk were killed during winter at four to five times the level they were killed during either calving or the rut. The vulnerability of adult elk to cougar predation increased as indicated by their larger proportion, and greater proportion in poor condition, in the cougar diet as winter progressed. Bull elk likely entered winter in an already compromised condition because of the considerable energy expended during contests for females while in the rut; thus their condition may have declined more rapidly than that of females as winter progressed (Atwood et al. 2007; Metz 2010).

**TABLE 5.3.** Proportion of elk calves (<12 months), prime-age adult cows (1–14 years), old cows (>15 years), and bulls killed by cougars prior to wolves (1988–94, cougars  $n = 188$ ); by cougars and wolves during early wolf restoration (1998–2001, cougars  $n = 129$ , wolves  $n = 593$ ); and once wolves had colonized (2002–5, cougars  $n = 186$ , wolves  $n = 641$ ) on the Greater Yellowstone Northern Range, Montana and Wyoming.

| Study Phase            | Calves  |        | Adult Cows |        | Old Cows |        | Bulls   |        |
|------------------------|---------|--------|------------|--------|----------|--------|---------|--------|
|                        | Cougars | Wolves | Cougars    | Wolves | Cougars  | Wolves | Cougars | Wolves |
| Pre-wolf               | 0.66    |        | 0.22       |        |          |        | 0.09    |        |
| Early wolf restoration | 0.68    | 0.40   | 0.16       | 0.21   | 0.07     | 0.14   | 0.09    | 0.25   |
| Wolves colonized       | 0.50    | 0.31   | 0.27       | 0.21   | 0.13     | 0.13   | 0.10    | 0.36   |

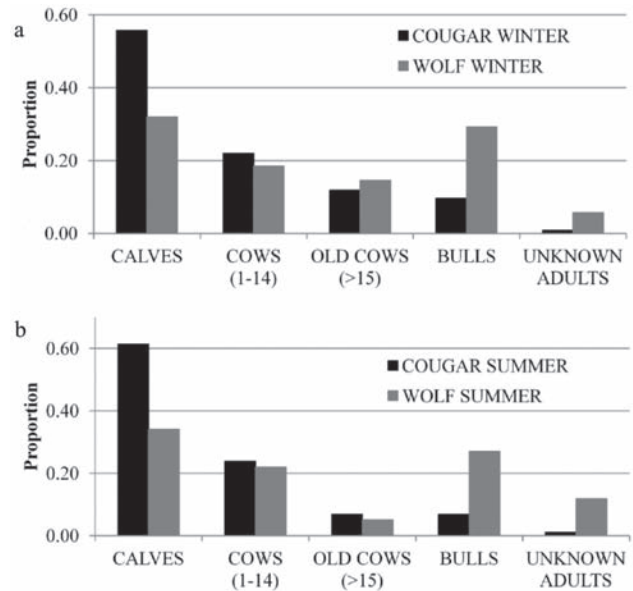


**FIGURE 5.4.** Proportion of adult female and male elk in the diet of cougars at three times of year during the wolf restoration study, 1998–2005: winter (December–April,  $n = 105$ ), birth/calving period (May–July,  $n = 26$ ), during the rut (September–November,  $n = 19$ ).

### Cougar and Wolf Prey Selection Compared

Although we worked year-round to accumulate information on cougar kills, in our DW study we documented 22 percent and 29 percent of the number of wolf kills collected in winter and summer, respectively. The proportion of elk calves, cows, old cows, and bulls killed by DW cougars was similar in winter and summer (fig. 5.5) [6]. For wolf kills the proportion of calves, prime-age cows, and bulls was likewise similar in winter and summer, differing only for old cows (fig. 5.5) [7]. During wolf restoration we found annual differences, as cougars killed an equal to greater proportion of adult elk starting in 2002, and we therefore collapsed data into two time periods, early wolf restoration (1998–2001) and wolves established (2002–5), for further assessing cougar prey selection of calves, cows, and bulls [8].

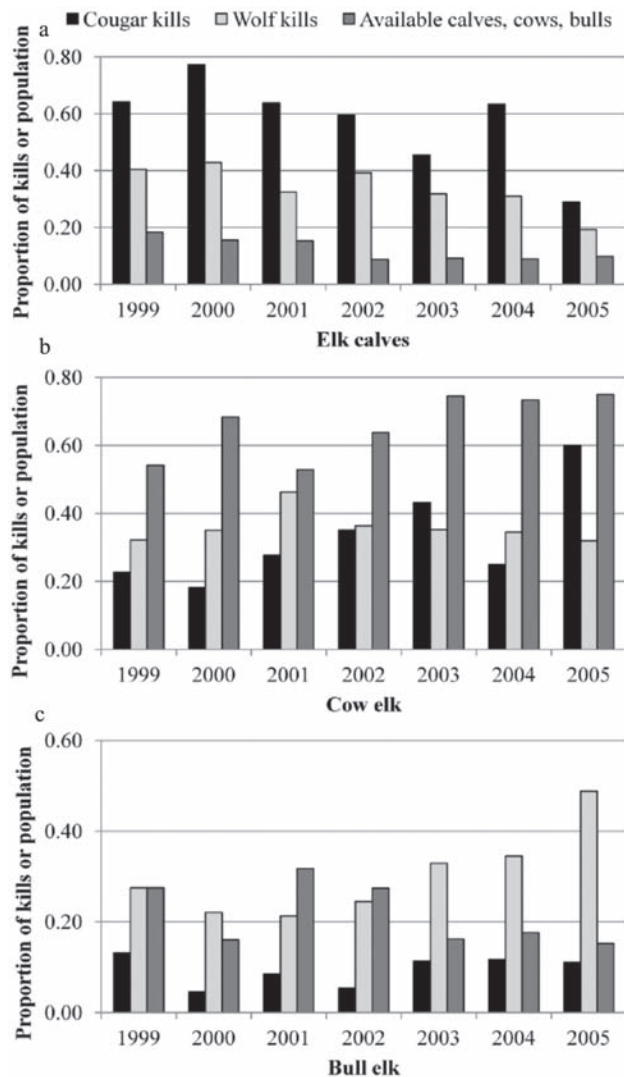
In figure 5.6a we see that cougars and wolves killed elk calves more often than expected relative to their abundance each year, both during early wolf restoration and after wolves were colonized [9]. Cougars killed cow and bull elk less often than expected based on their abundance, and wolves also did not show preference for cows in any of the study



**FIGURE 5.5.** Sex-age class of elk killed by cougars and wolves on Greater Yellowstone's Northern Range, 1998 through 2005, (a) in winter (cougars  $n = 228$ , wolves  $n = 1,032$ ) and (b) during non-winter (cougars  $n = 88$ , wolves  $n = 296$ ).

years. In the early years of wolf restoration, wolves did not show strong selection for bulls, but that changed after wolves became established. During the years 2003 through 2005, wolves killed bulls in greater proportion than the abundance of bulls (fig. 5.6b, 5.6c) [10].

These results helped inform comparisons of diets of cougars and wolves. During both early restoration and established periods, cougars killed a substantially greater proportion of calves and a smaller proportion of bull elk than did wolves (table 5.3) [11]. Around 2002 and in the following years, both carnivores killed proportionally fewer calves. During this time the proportion of bulls increased in the diet of wolves, and the proportion of prime-age cows increased



**FIGURE 5.6.** Sex-age class of elk killed by cougars and wolves versus estimated availability of calf (a), cow (b), and bull (c) elk on the Greater Yellowstone Northern Range, 1999–2005. Note that both cougars ( $n = 228$ ) and wolves ( $n = 1,032$ ) killed elk calves (a) more often than expected based on calf abundance. Cougars killed cow and bull elk (b, c) less often than expected based on abundance.

in the diet of cougars (table 5.3; Smith and Bangs 2009) [12]. These results suggested that (1) the condition of adult elk declined, resulting in their increased vulnerability to cougars; or (2) the availability of calves declined, and cougars switched to killing cows; or (3) both of these conditions arose in the later years of our study. We explore these ideas in more detail in the discussion that follows.

## HEALTH OF ELK KILLED BY COUGARS AND WOLVES

At the same time our study was under way, another study was assessing the condition of cow elk on the Northern Range. The femur marrow fat of most Northern Yellowstone cows was above 85 percent during February and March—values that indicated good to excellent survival probability through the rest of winter (R. Cook et al. 2001; J. Cook et al. 2004). Cow elk with femur marrow fat values less than 85 percent were in overall poor condition. Further, a study in 2000–2001 revealed that about 4 percent of northern Yellowstone cow elk had less than or equal to 2 percent body fat during winter, which was equivalent to femur marrow fat less than or equal to 40 percent, corresponding to a level of condition with relatively high probability of death as a result of winter starvation (R. Cook et al. 2004).

Using these values as a rule of thumb for all elk, we found that in summer, June through October, cougars killed elk in good condition—with average femur marrow fat of 87 percent ( $SE = 3.5$ ) for calves and 86 percent ( $SE = 1.7$ ) for cows. In winter roughly 30 percent (52 of 175) of cougar-killed elk and 32 percent (180 of 556) of wolf-killed elk had femur fat above 85 percent, reflecting good survival probability through winter. The remaining 70 percent and 68 percent of elk killed by cougars and wolves during winter, respectively, were in poor condition, with femur marrow fat less than 85 percent. Roughly 23 percent (40 of 175) of the cougar-killed elk and 30 percent (178 of 556) of wolf-killed elk had femur fat values less than 41 percent, were unlikely to have survived through winter, and had increased vulnerability to predation because of their poor condition. The remainder of cougar-killed elk (47%) and wolf-killed elk (36%) were in relatively poor condition (femur fat of 41–85 percent), suggesting they were more vulnerable to predation than their healthier counterparts. When we limited data to cow elk, cougars killed cows with femur fat of less than 41 percent and in proportion to their expected availability, while wolves killed more cows in poor condition relative to their expected availability based on the findings of R. Cook and colleagues (2004) that 4 percent of sampled cows were at this level of condition during winter [13].

Because adult elk were more likely to be killed in winter than in summer, as related to their poorer nutritional condition, we looked more closely at cougar- and wolf-killed elk during winter. We tested for differences in condition using



**TABLE 5.4.** Logistic regression models of variables predicting the likelihood of kills being made by cougars versus wolves, where wolves are the reference cell in model selection.

| Model <sup>a</sup>       | Model Selection |        |        |   |                |                | Odds Ratio (95% CI) |                                 |              |                          |
|--------------------------|-----------------|--------|--------|---|----------------|----------------|---------------------|---------------------------------|--------------|--------------------------|
|                          | Log Likelihood  | AIC    | ΔAIC   | K | w <sub>i</sub> | Evidence Ratio | Calf                | Sex_Age <sup>b</sup><br>Old Cow | Bull         | FMF <sup>c</sup><br>≤41% |
| INT + SEX_AGE + FAT_LT41 | −340.08         | 692.16 | 0      | 6 | 0.92           |                | 2.67                | 2.10                            | 5.46         | 2.08                     |
| INT + SEX_AGE + %FAT     | −342.95         | 697.89 | 5.73   | 6 | 0.05           | 17.57          | (1.68–4.26)         | (1.21–3.66)                     | (2.86–10.42) | (1.34–3.22)              |
| INT + SEX_AGE + ASIN_FAT | −343.95         | 699.89 | 7.73   | 6 | 0.02           | 47.72          |                     |                                 |              |                          |
| INT + SEX_AGE            | −345.78         | 701.56 | 9.40   | 5 | 0.01           | 110.18         |                     |                                 |              |                          |
| INT + FAT_LT41           | −395.73         | 797.47 | 105.31 | 3 | 0.00           |                |                     |                                 |              |                          |
| INTERCEPT ONLY           | −397.98         | 799.97 | 107.81 | 2 | 0.00           |                |                     |                                 |              |                          |
| INT + %FAT               | −397.25         | 800.50 | 108.34 | 3 | 0.00           |                |                     |                                 |              |                          |
| INT + ASIN_FAT           | −397.73         | 801.47 | 109.31 | 3 | 0.00           |                |                     |                                 |              |                          |

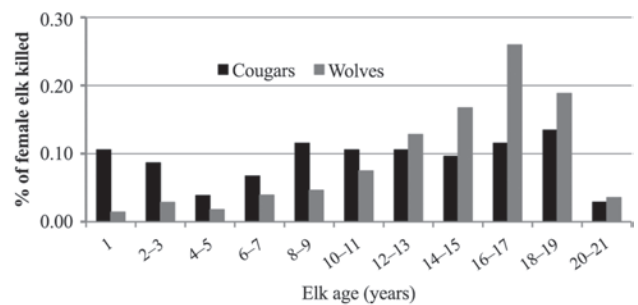
<sup>a</sup> In this model set,  $n/K = 120.5$ .

<sup>b</sup> Model design coded with adult cow elk as the reference. For ease of interpretation, odds ratios are presented as  $>1.0$  (equally likely outcome) with the following interpretations: elk calves were nearly 3 times more likely than adult cows to be killed by cougars; old cows were nearly 2 times as likely and bulls were 5 times as likely as adult cows to be killed by wolves.

<sup>c</sup> Relative to elk killed by cougars, odds were 2 times greater that an elk killed by wolves was in poor condition (femur marrow fat, FMF, less than 41%) and unlikely to survive winter.

percentage of femur marrow fat and analysis of variance and generalized linear models (GLM) with fixed factors of predator species, winter month (Nov, Dec, Jan, Feb, Mar, Apr), and sex-age class (calf, prime adult female, old adult female, bull) of elk killed. We normalized elk femur marrow fat values via arcsine of the square root transformation (Krebs 1999). Femur marrow fat comparisons were limited to 175 of 249 (70%) winter cougar kills and 556 of 1,141 (49%) winter wolf kills where we were able to assess gender, age, and femur fat.

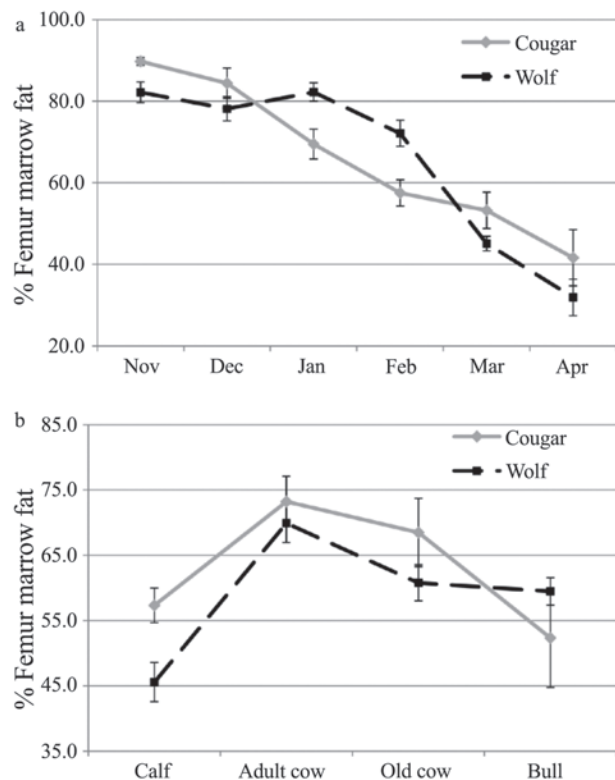
Logistic regression revealed that the sex-age class and condition of elk influenced patterns of prey selection by cougars and wolves (table 5.4). Cougars were somewhat more likely ( $2 \times$  odds) to prey on elk calves, again supporting predictions that young elk were particularly vulnerable to cougars—at least somewhat more vulnerable to cougars than they were to wolves—whereas size of adult elk reduced their vulnerability to cougars (Murphy 1998; Murphy and Ruth 2010). Although cougars killed proportionally fewer cow elk than wolves did up until 2002, we found that cougars killed prime-age cows that were 9 to 12 years of age (95% confidence interval around the mean) whereas wolves rarely did—they killed cows 14 to 15 years of age (95% CI; fig. 5.7). Wolves were slightly more likely to prey on older cow elk ( $2 \times$ ) than were cougars, yet the mean age of those old cows killed by wolves and cougars was the same—17



**FIGURE 5.7.** Age distribution of cougar- ( $n = 104$ ) and wolf-killed ( $n = 281$ ) female elk on the Greater Yellowstone Northern Range, 1998–2005, showing wolves focused predation on elk fourteen years old and older compared to cougars. Cougars killed primarily elk calves (see fig. 5.5). Excluding calf kills, sample sizes for cow elk are small:  $<15$  for cougar-killed cow elk in each age group and  $<30$  for wolf-killed elk ages 1 through 14.

years old [14]. Wolves were substantially more likely to prey on bull elk ( $5 \times$ ) compared to cougars. The mean age of bulls killed by cougars was 4.3 (95% CI = 2.0–6.6,  $n = 14$ ), while mean age of bulls killed by wolves was 7.8 (95% CI = 7.3–8.3,  $n = 190$ ).

The condition of adult elk contributed to their vulnerability to both predators, with cougars and wolves killing elk in similar condition through winter (fig. 5.8a) [15]. Despite this finding, elk with femur marrow fat less than 41 percent



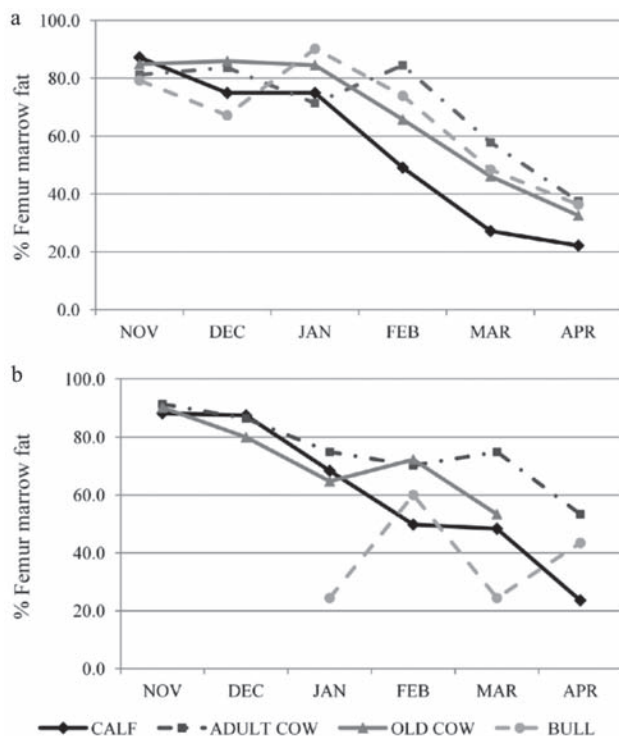
**FIGURE 5.8.** Percent femur marrow fat by month (a) and by sex-age class (b) of elk killed by cougars and wolves in winter on the Greater Yellowstone Northern Range, 1998–2005. Bars represent the standard error of the estimate for 175 cougar kills and 556 wolf kills in a and 174 cougar and 549 wolf kills in b.

were slightly more likely to end up in the diet of wolves than in that of cougars, consistent with other research findings (Husseman et al. 2003a; Atwood et al. 2007). Wolves killed calf elk with femur marrow fat values averaging 12 percent less than calves killed by cougars (fig. 5.8b). Femur marrow fat of prime-age cows killed by the two carnivores differed little, while old cows killed by wolves had femur fat values averaging 7 percent less than those killed by cougars. On average, the femur marrow fat of bulls killed by cougars was about 7 percent lower than femur marrow fat of wolf-killed bulls (fig. 5.8b).

Calves, old cows, and bulls killed by wolves reflected a rapidly declining condition beginning in January (fig. 5.9a), which was much earlier than the dramatic decline in condition of both cougar- and wolf-killed elk occurring in March,

as noted by Husseman and co-workers (2003b) during their Idaho study. Bull elk appeared in the kills of cougars only in late winter, when they became more vulnerable to predation because of poor condition (fig. 5.9b). Regardless of the discrepancies found in the values of femur marrow fat between cougar- and wolf-killed prey, as winter progressed the condition of prey equated to decreased chances of those individuals surviving the winter, indicating that both carnivores selected relatively similar prey.

Ungulates can become injured during effective escape from encounters with predators; through interactions with conspecifics, as when bulls engage each other during rut; or from natural accidents (Ross et al. 1997). Following wolf project protocols, we inspected cougar kills for arthritis in the vertebral column and pelvic-femur ball socket as well as necrosis of the mandibles and injuries such as breaks and swelling in bones and joints. We also looked for signs of exoparasites, including ticks (*Ixodes* sp.) and fleas



**FIGURE 5.9.** Average percent femur fat by sex-age class and month elk killed by wolves (a,  $n = 549$ ) and cougars (b,  $n = 174$ ) on Greater Yellowstone's Northern Range, winters 1998–2005.



**FIGURE 5.10.** Swollen phalanges-metatarsal joint of a cow elk killed by a female cougar on the Greater Yellowstone Northern Range. The swollen joint impeded full range of motion and limited the mobility of this individual. Photo by Toni Ruth, Hornocker Wildlife Institute/Wildlife Conservation Society.

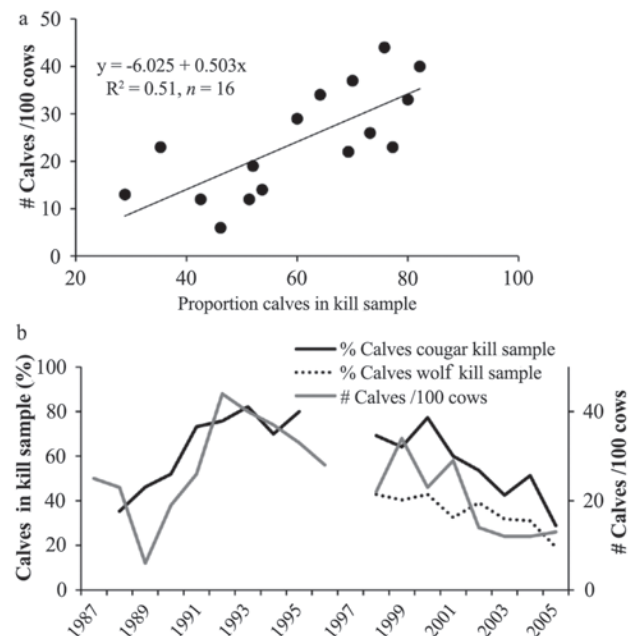
(*Ctenocephalides* sp.), and endoparasites such as tapeworms (*Echinococcus granulosus*), botfly larvae (*Cephenemyia* sp.), and lungworm (*Dictyocaulus* sp.; Worley and Barrett 1962).

We documented injuries and abnormalities in 9 percent of all ungulate prey killed by cougars, which included twenty cow elk, twelve elk calves, two bull elk, two mule deer, and one bighorn sheep (see fig. 5.10). Injuries and abnormalities observed included calcification of metatarsus, tibia, and ribs from previous breaks; swollen tarsal-metatarsal joints; and a metatarsal-hoof joint tumor. Thirteen adult elk with injuries, arthritis, and joint abnormalities averaged 11.5 years old ( $SE = 1.8$ ) and had femur fat values that averaged 53 percent ( $SE = 9.4$ )—the same mean and median age (11.7 years,  $SE = 1.5$ ) and femur fat (57%,  $SE = 8.0$ ) as eleven adult elk documented with parasites [16]. Elk calves with injuries and parasites were also in similarly poor nutritional condition (36% and 41% average femur fat, respectively) and were unlikely to have survived [17]. While underrepresented in our study and documented in few other studies, injuries, parasites, or other disease likely further compromised individuals and increased their vulnerability to cougars and wolves during severe and late winter conditions.

## DID COUGARS SWITCH FROM CALVES TO ADULT ELK?

To reduce competition with wolves for similar prey as elk declined, cougars might exploit alternate food sources by switching to less abundant prey—an expected outcome for coexisting species responding to increasingly limited food resources (Murdoch 1969; Wiens 1993; Sinclair et al. 1998; Kortello et al. 2007; Murphy and Ruth 2010). One scenario of prey switching could arise if cougars and wolves competed strongly for elk calves and calf numbers declined. In this case we expected cougars to switch to more abundant adult elk. Because adult elk were formidable prey, cougars might also switch to more vulnerable ungulate prey species such as pronghorn, bighorn sheep, or mule deer.

Across the years of our PW and DW studies on the Greater Yellowstone Northern Range, the diet of cougars reflected a linear relationship to changes in the elk calf:cow



**FIGURE 5.11.** Relationship between the elk calf:cow ratio and the proportion of calves in the cougar kill sample using linear regression for sixteen years spanning the pre-wolf and during wolf studies (a). The trend in the calf:cow ratio and the proportion of calves in the cougar and wolf sample are shown in (b). Both indicate that the diet of cougars and wolves changed as the ratio of calves to cows declined, with proportionally fewer calves and more adult elk making up the diet of both carnivores.

ratio (fig. 5.11a) [18]. The ratio of calves to cows declined as our study progressed: the mean ratio of 12–14 calves per 100 cows during the years 2002–5 was less than the average of 31 calves per 100 cows observed during the period 1968–2001 (Cross et al. 2009). This decline translated to an average of 1 calf per every 4 adult elk across the years of the PW study, but it eventually averaged 1 calf per every 7 adult elk across the years of the DW study. As calves became less available to cougars and wolves, they made up a declining proportion of both carnivores' diets relative to adult elk (fig. 5.11b). This response suggested that cougars and wolves may have switched to adult elk as calves declined.

To evaluate quantitatively the existence of prey switching by cougars, we regressed the ratio of adult elk and calves in cougar diets to the ratio of adult elk and calves available in the population using Murdoch's (1969) selection coefficient, modified to allow changes in diet with changes in relative availability of different types of prey as follows (Greenwood and Elton 1979; Garrott et al. 2007; Becker et al. 2009a):

$$\frac{g_{\text{adult elk}}}{g_{\text{calves}}} = \left( c \frac{N_{\text{adult elk}}}{N_{\text{calves}}} \right)^b$$

The ratio of adult elk to elk calves in the diet of cougars is reflected on the left side of the equation. The right side of the equation is the ratio of adult elk to calves in the elk population. Values of the proportionality constant,  $c$ , less than 1 indicate preference for prey, whereas the variable  $b$  is a measure of the extent of prey switching. Values of  $b$  greater than 1 indicate switching.

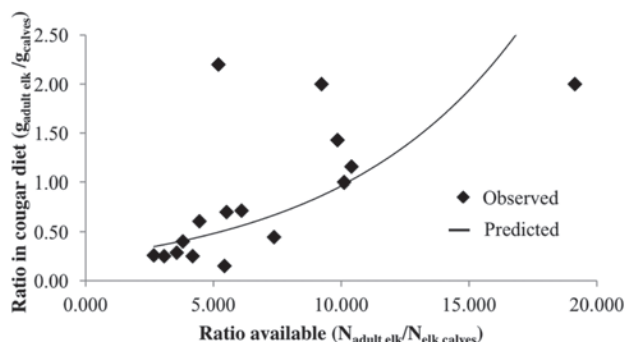
We found a curvilinear relationship, with preference for calves over adult elk at low adult:calf ratios. As the ratio of

adults to calves increased, the curvilinear relationship supported the notion that cougars switched their diet from calves to adult prey (fig. 5.12) [19]. Yet data collected at the beginning and end of our study in 1998 and 2005, respectively, appeared to have considerable influence on the relationship. Once we removed data associated with these two years, the effect of prey switching was reduced [20]. These findings indicated that prey selection by cougars and wolves remained driven primarily by a strong preference for the most vulnerable prey, elk calves, with increased preference for differing sexes of adult elk related to declining calf:adult ratios and vulnerability of adults in late winter. Greater predation on cows by cougars and on bulls by wolves provided evidence that both carnivores became additive influences on the portion of the elk population with the greatest reproductive value. However, a proportion of this mortality could be considered compensatory because at least 11 percent to 15 percent of elk killed by both cougars and wolves were unlikely to have survived the winter.

## OTHER PREY

Small non-ungulate prey and other carnivores were killed by cougars and wolves during summer and winter, but we located few of these prey because they were consumed quickly and more completely; they were also underestimated by our kill sampling methods. Coyote, red fox, marmot, porcupine, snowshoe hare, cottontail rabbit, red squirrel, chipmunk, mice, a golden eagle, and a saw-whet owl made up 19 percent and 8 percent of the documented diet of cougars prior to and during wolf restoration, respectively (table 5.2). In addition to these species, badgers, a sandhill crane, a short-eared owl, and a raven made up 8 percent of the diet of wolves during our study (Smith et al. 2006).

Other ungulates occurred in substantially lower numbers than elk and were rarely killed by cougars or wolves (Yellowstone National Park 2008; Cross et al. 2009). Combined, bighorn sheep, pronghorn, moose, and mountain goats made up 3 percent of the 312 cougar kills documented prior to wolf presence and 5 percent of 468 kills we documented during wolf presence, suggesting that cougars did not substantially increase their predation on other species in the DW period (table 5.1). The massive size, horns, and group foraging in open areas of bison imposed limitations on cougars' ability to kill them, and bison were not documented as cougar prey in either study phase (Murphy 1998).



**FIGURE 5.12.** Observed versus predicted relationship between the ratio of adult elk:calves on the Greater Yellowstone Northern Range and the ratio of adult elk:calves in the diet of cougars, 1998–2005.



Pronghorn, moose, and bison were also killed infrequently by wolves, making up 2 percent of the 1,450 documented ungulate kills made by wolves during our study. Because pronghorn and bighorn sheep posed special concern to park managers (Yellowstone National Park 1997), including the potential for predation by cougars and wolves (fig. 5.2b) to influence their small populations, we address predation on these two species in more detail.

### Pronghorn

The small population of pronghorn was of special interest because their numbers have at times been very low, causing concerns over their genetic well-being and their long-term survival as a population entity (Yellowstone National Park 1997). With predation risk, loss of northward migration, and poor winter range conditions as principal concerns, the National Park Service listed pronghorn as a species of special concern (National Research Council 2002; Boccadori et al. 2008). A resident proportion of pronghorn occupied lower-elevation winter range year-round for foraging, birthing, and fawn rearing. Another proportion of pronghorn migrated from lower-elevation winter range to summering areas at higher elevations—1,500 to 2,500 meters—between April and October each year. These higher-elevation areas were characterized by mixed habitat types and reduced visibility for detection of predators by pronghorn (White et al. 2007; Boccadori et al. 2008; Barnowe-Meyer et al. 2009).

During the PW study, Murphy (1998) documented a single male pronghorn killed by a female cougar in sage-steppe habitat, which constituted 0.3 percent of all prey and 0.4 percent of ungulate prey killed by cougars. As wolves were restored to the Greater Yellowstone landscape, prior to June 2002 pronghorn comprised a similarly small proportion of cougar kills, at 0.4 percent (1 of 230). Yet by November 2004, that percentage had increased to 2.1 percent of all prey (10 of 468) and 2.3 percent of ungulate prey (10 of 432) killed. This suggests that perhaps as wolf densities peaked and elk calf:cow ratios declined, cougars were switching to various alternative prey, including pronghorn. However, a single female cougar was responsible for 70 percent of the kills, suggesting preference for pronghorn by this individual or that her access to pronghorn within her home range increased at certain times. The remaining two female pronghorn were killed by two other adult female cougars. Except for an adult

male pronghorn and a four- to five-month-old male fawn, all pronghorn killed were newborn fawns, pregnant does, or does that had recently given birth.

Although pronghorn made up a very low proportion of the cougar diet during our studies, cougars were the second most common source of predation (14% of known deaths) in a study assessing cause-specific mortality of adult pronghorn in our study area (Barnowe-Meyer et al. 2009). Three of the radio-collared pronghorn were part of our ten documented cougar kills. At least three factors may influence the vulnerability of pronghorn to cougar predation on the Greater Yellowstone Northern Range: (1) use of structurally complex and mixed habitat types during migration and parturition (Ockenfels 1994; Logan and Sweanor 2001; Anderson and Lindzey 2003; White et al. 2007); (2) avoidance of coyotes, the principal cause of mortality, during parturition; and (3) behavior of individual cougars that were adept at killing pronghorn.

First, between 1999 and 2004, six female pronghorn were killed by cougars during spring migration (May to June) and two male and two female pronghorn were killed during fall migration (August to October). Migrant pronghorn traversed narrow nonforested corridors, and cougars killed pronghorn does in areas of steep and rocky terrain with mixed sagebrush and tree cover or very close to these types of cover on Mount Everts, the Oxbow-Geode Plateau, and along Specimen Ridge. In these habitats pronghorn faced increased risk of predation from cougars, as their usual predator-avoidance behaviors were likely hindered by reduced visibility in forested habitat and reduced ability to flee in rugged terrain (Byers 1997). Apparently, a greater proportion of the pronghorn population was vulnerable to cougar predation in the DW study period—20 percent to 25 percent of the pronghorn population migrated in the PW study phase compared to almost 70 percent of pronghorn migrating during 1999 through 2006 (White et al. 2007).

Second, all does killed during spring migration were either pregnant or had recently given birth. This resulted in the death of four fetuses with their two mothers, one fawn killed at the same time as its mother, and the orphaning of at least two fawns with the death of their mothers. In combination, migration and parturition may have nutritional costs for adult female pronghorn. Three females had femur marrow fat of 58 percent, 62 percent, and 71 percent, respectively, when killed in June, while two females had femur

marrow fat values of 99 percent and 68 percent in August and September, respectively, indicating that five of the six were likely struggling nutritionally. Because coyotes were responsible for 56 percent of predation on adult females and up to 43 percent to 79 percent of fawn predation, migrant female pronghorn potentially selected rugged and densely vegetated areas to avoid predation by coyotes on newborn fawns (Byers 1997). In avoiding coyotes the normal defense against smaller predators by female pronghorn might be less effective against stalking behavior of cougars (Soluk 1993; Byers 1997; Losey and Denno 1998; Atwood et al. 2007, 2009). Cougars also preyed heavily on elk calves during the pronghorn fawning season and potentially posed a heightened risk to pronghorn fawns in places that overlapped elk calving areas (Barber-Meyer et al. 2008; Barnowe-Meyer et al. 2009). Despite a greater diversity of carnivores residing in areas used by migrant pronghorn, migrant fawn survival exceeded that of non-migrants (Barnowe-Meyer et al. 2009).

Lastly, individual cougar behavior influenced the outcome of predation on pronghorn (see Ross et al. 1997; Logan and Sweanor 2001; Murphy and Ruth 2010). The typically low rates of cougar predation on pronghorn that we found, primarily associated with migration, suggested that cougar predation may be largely opportunistic. Our kill rate sampling of eleven adult cougars during all seasons of our DW study should have led to a fairly unbiased sampling of kills by female cougars. Further, pronghorn migrated through home ranges of multiple cougars, suggesting that one female, F125, had a particular knack for killing pronghorn (see text box 5.1).

In the PW study, 1988 to 1993, pronghorn numbered from 400 to nearly 600 individuals. No aerial counts were conducted in 1994. Pronghorn numbers were considerably lower during aerial surveys from 1995 through 2006—between 169 and 235 (fig. 5.2b). Considering that about 70 percent of pronghorn were migratory during the later study period, we estimated that roughly 118 to 164 pronghorn migrated to higher-elevation areas each year between 1999 and 2006. Thus offtake of pronghorn by cougars was, at a minimum, between 0.6 and 4 percent each year during migration periods. Once they returned to low-elevation winter range, pronghorn were apparently not vulnerable to cougar predation. Similar to the situation with cougars, pronghorn made up a small percentage—less than 1 percent—of the summer diet of wolves, with a total of seven pronghorn killed by

Northern Range packs during summers over the course of our study (Smith et al. 2007). Although the matter is still under investigation, it appears that predation by cougars, wolves, and coyotes, in combination, may act to limit growth of the pronghorn population (Barnowe-Meyer et al. 2009).

### Bighorn Sheep

Numbering between 200 and 250, bighorn sheep occurred in ten to thirteen interbreeding bands, occupying steep cliffs along the upper Yellowstone River (fig. 5.2b; White et al. 2008). Bighorn sheep were present year-round but wintered in low-elevation habitats along the Yellowstone River near Mammoth and Gardiner and then migrated during May through October to higher-elevation ranges in the western portion of the Greater Yellowstone Northern Range (Yellowstone National Park 1997; White et al. 2008). As with pronghorn, we documented bighorn sheep infrequently in the diet of cougars. Bighorn sheep made up 2 percent of the cougar diet during winter in both study phases and 3 percent of the cougar summer diet during wolf presence (table 5.1). Cougars usually killed bighorn sheep in or near broken terrain, rock outcrops, deadfall, or cliffs along the Yellowstone and Lamar Rivers. They killed sheep in both good and poor condition during all seasons. Femur marrow fat values collected from eight sheep in the DW study ranged from 95 percent to 96 percent for two rams killed in August and November to 41 percent for a ewe killed in April and 16 percent for a ram killed in July. This suggested to us that cougar predation on bighorn sheep during our study was largely opportunistic.

In contrast to specialized predation by a few individual cougars observed in many bighorn sheep populations (Ross et al. 1997; Logan and Sweanor 2001; Murphy and Ruth 2010) and the specialized predation we noted by one female cougar on pronghorn, bighorn sheep during our study were killed by a number of individual cougars. Two female cougars and one male killed three bighorn in three different years prior to wolves, whereas six female and three male cougars killed twelve bighorn sheep sporadically across six years of our DW presence study. All sheep were adults, with almost an even split between rams and ewes.

The effects of predation are often a concern for bighorn sheep because they occur in small groups at low densities in various ecosystems and are prone to reductions and increased predation vulnerability from disease (e.g., scabies

mite, pink-eye, and pneumonia—Wehausen 1996; Ross et al. 1997; Krausman and Shackleton 2000; Logan and Sweanor 2001; Ernest et al. 2002; Rominger et al. 2004). Prior to our DW study, counts of bighorn sheep decreased following a severe winter in 1997 but then increased and remained within 10–20 percent of the 213 sheep counted when wolves were restored (White et al. 2008). Although wolf numbers increased following restoration, they did not kill any bighorn sheep during our study, and bighorn sheep numbers grew to 363 by 2011. The bighorn sheep population in and near Yellowstone National Park was little affected by cougars or by the restoration of wolves (Murphy 1998; White et al. 2008).

### CHARACTERISTICS OF KILL SITES

In this section we investigate the influence of landscape characteristics in mediating predation on elk by cougars and wolves. We expected that compared to kill sites of wolves, cougar kills would occur in rougher terrain, closer to hunting cover and escape terrain of trees and rocks, in areas of less snow, and more often in the core area—the area used most intensively within the cougar's home range. If, in avoiding wolves, elk used more structurally complex habitat, thus facilitating predation by cougars, we expected cougar kills to occur in more topographically complex and forested areas than cougar kills prior to wolves (Soluk 1993; Byers 1997; Losey and Denno 1998; Atwood et al. 2009).

Although homogeneous habitats of more extensive forested cover can limit the coursing behavior of wolves, resulting in less disparity between stalking and pursuit of predators, we did not expect this outcome in our study area (Murray et al. 1994; Kunkel et al. 1999). A matrix of open grassy valleys and plateaus interspersed with forested and rugged terrain predominated across the Greater Yellowstone Northern Range. This heterogeneity was relevant to the scale at which wolves and cougars successfully pursued and captured prey (Creel and Creel 2002). Wolf project field crews observed forty-six chases of elk that led to successful kills by wolves. These observations revealed that chase distances averaged  $978.2 \pm 141.73$  meters (SE) on the Northern Range (Kauffman et al. 2007). Wolves rarely chased prey in a straight line, and distances reflected minima between where wolves initiated pursuit of prey and where prey were killed.

In contrast, cougars sometimes quickly killed small ungulate prey where they were encountered, including bedded

prey. Because of their larger size and attempts to dislodge the cougar, adult elk and adult bighorn sheep traveled greater distances—up to 150 to 300 meters—before being killed. While investigating kills, we were able to determine for only relatively few sites the point where a cougar ambushed prey and whether the prey was dragged a distance to another location. As a result, in this section we use the term *kill site* to refer to the final resting site where most of the carcass was consumed by a cougar or a pack of wolves. After making the kill, cougars sometimes moved prey and concealed it away from the kill site, and scavengers also moved some carcasses from the initial site of death, yet we assumed these distances to have negligible influence on comparisons of kill sites. For 203 sites where we had clear details of kill and cache sites, prey carcasses were discovered an average of 49 meters (95% CI = 40 to 57 meters) distant from where prey were killed.

To address the hypothesized differences in ambush versus chases leading to kills, we examined environmental characteristics of kills at two spatial scales: (1) the point location where the prey was considered killed and (2) at the upper 95 percent confidence interval of 1,260 meters for wolf chase distance, to encompass where prey were potentially encountered during hunting. Thus at the second scale we looked at environmental characteristics within a 1,260 meter radius around the kill site.

During our investigations of kills and kill sites, we recorded coordinates (Universal Transverse Mercator), prey species and age, cover type classed as forest or nonforest (Despain 1990), elevation, and slope. We explored several indices of topographic roughness, which we discuss in appendix E. Based on weight at death, ungulate prey were grouped into two size classes: large (avg. =  $240 \pm 20.7$  kg; adult elk) and small (avg. =  $80.9 \pm 33.7$  kg; elk calves and all mule deer, bighorn sheep, and pronghorn). We compared summer and winter kill sites of PW and DW cougars, but we limited kill site comparisons between cougars and wolves to winter kills because the best quantitative data on wolf predation were restricted to winter during our study.

To determine which environmental variables were the best predictors of whether a kill was made by a cougar or a wolf, we examined a set of forty logistic regression models. Certain variables were strongly related to each other and therefore were not included in the same model [21]. Following Burnham and Anderson's (2002) guidelines, we used the Akaike Information Criterion (AIC), ranked mod-

els, and assessed model selection uncertainty to determine which logistic regression models best explained patterns of resource use across the study area. We compared the 95 percent confidence intervals of each variable to evaluate if the coefficients were statistically different between the PW and DW time periods.

### Kill Sites of Cougars and Wolves

As predicted, cougar kill sites occurred in more forested and rougher terrain than wolf kill sites (7 times more likely to be forested; 922 times more likely to be in rough terrain), reflecting cougars' preferential use of cover to capture prey and to conceal the kill from competitors (table 5.5) [22]. Wolves were somewhat more likely to kill prey in areas of greater elk use than were cougars, and wolves' relatively long chases ended with kills in more open habitat on lesser slopes and in deeper snow (fig. 5.13a). Wolves typically killed prey 81

to 97 meters (95 percent confidence interval) from forested or rocky terrain compared to cougar kills, which occurred 12 to 22 meters from forested or rocky terrain.

Incorporating the chase distance of wolves confirmed that wolves successfully subdued prey farther from forested or rocky terrain. At this larger scale, the importance of areas with greater elk use was more apparent—wolf kills were more likely to occur in areas of greater elk use compared to where cougars killed prey (fig. 5.13a). Wolves killed prey in twice the mean snow depth compared to where cougars killed prey. Wolves were apparently better able to negotiate greater snow depths, perhaps because of their longer legs and the reduced ability of prey to escape chase (Lima 1992; Husseman et al. 2003b). Another explanation could be that habitats that provide escape and hunting cover for cougars during winter are those occurring at lower elevations with greater slope exposure, where snow accumulations are less

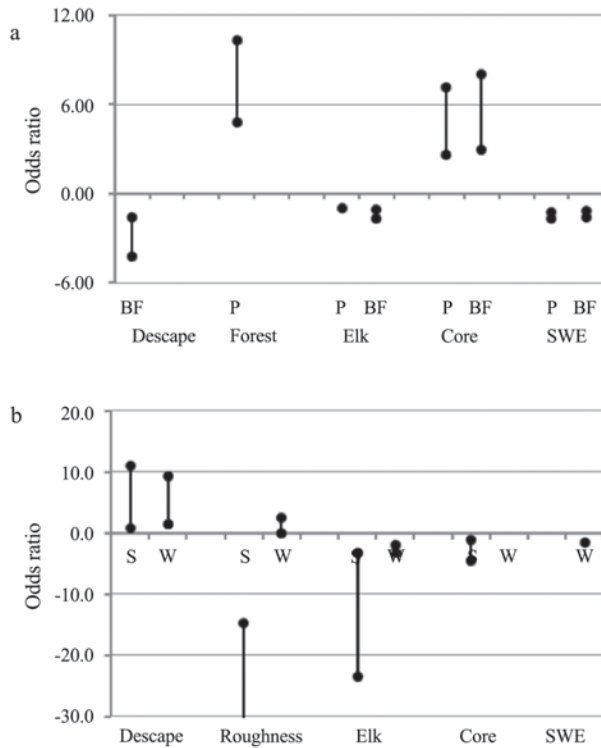
**TABLE 5.5.** Top logistic regression models explaining variation in cougar kill sites during wolf restoration (DW) compared to pre-wolf cougar kill sites and wolf kill sites on the Greater Yellowstone Northern Range, 1998–2005. Cougar and wolf kill site comparisons are winter only.

| <i>Kill Site Comparison<sup>a</sup></i>                   | <i>K</i> | <i>AIC</i> | $\Delta AIC$ | <i>wi</i> | <i>AUC<sup>b</sup></i> |
|-----------------------------------------------------------|----------|------------|--------------|-----------|------------------------|
| Cougar–cougar summer                                      |          |            |              |           |                        |
| DESCAPE + RGHASP + ELK + CORE                             | 6        | 212.81     | 0.0          | 0.42      | 0.77                   |
| DESCAPE + RGHASP + ELK                                    | 5        | 215.13     | 2.3          | 0.13      | 0.76                   |
| DESCAPE + RGHASP + RGHASPSQ + ELK + ELKSQ + CORE          | 8        | 215.62     | 2.8          | 0.10      | 0.77                   |
| FOREST + RGHASP + STDELK + CORE                           | 5        | 216.12     | 3.3          | 0.08      | 0.76                   |
| Cougar–cougar winter                                      |          |            |              |           |                        |
| DESCAPE + ELK + ELKSQ + SWE                               | 6        | 503.72     | 0.0          | 0.38      | 0.54                   |
| DESCAPE + RGHASP + ELK + ELKSQ + SWE                      | 7        | 503.72     | 0.4          | 0.31      | 0.54                   |
| DESCAPE + RGHASP + RGHASPSQ + ELK + ELKSQ + SWE           | 8        | 503.72     | 2.4          | 0.11      | 0.51                   |
| DESCAPE + RGHASP + RGHASPSQ + STDELK + ELKSQ + CORE + SWE | 8        | 503.72     | 3.5          | 0.07      | 0.51                   |
| DW Cougar–wolf kill site (point)                          |          |            |              |           |                        |
| FOREST + RGHASP + ELK + CORE + SWE                        | 7        | 693.05     | 0.0          | 0.87      | 0.92                   |
| FOREST + RGHASP + RGHASPSQ + ELK + ELKSQ + CORE + SWE     | 9        | 696.81     | 3.8          | 0.13      | 0.92                   |
| FOREST + RGHASP + ELEV                                    | 5        | 715.30     | 22.2         | 0.00      | 0.90                   |
| DW Cougar–wolf kill site (buffered at 1,260 m)            |          |            |              |           |                        |
| DESCAPE + RGHASP + ELK + CORE + SWE                       | 7        | 625.37     | 0.0          | 0.80      | 0.92                   |
| DESCAPE + RGHASP + RGHASPSQ + ELK + ELKSQ + CORE + SWE    | 9        | 628.19     | 2.8          | 0.20      | 0.92                   |
| FOREST + RGHASP + ELK + CORE + SWE                        | 5        | 640.78     | 15.4         | 0.00      | 0.92                   |

<sup>a</sup> Variables are: DESCAPE = distance to nearest forest edge or rough terrain; FOREST = the number of forested 30 meter cells within a 240 meter buffer; RGHASP = terrain roughness variable ranging from zero to two, with two being the maximum topographical roughness possible and zero representing completely flat areas; RGHASPSQ = terrain roughness squared (quadratic term); ELK = values of elk use based on elk resource selection functions (Mao et al. 2005); ELKSQ = elk use squared (quadratic term); STDELK = standard deviation of elk use; SWE = snow water equivalent; CORE = kill was inside the cougar core use area. Variables are described in greater detail in appendix E.

<sup>b</sup> AUC = Receiver operating characteristics area under the curve providing an assessment of model fit.





**FIGURE 5.13.** Odds ratio and 95 percent confidence intervals (bars) of variables explaining variation in cougar kill sites during wolf restoration compared to kill sites of wolves (a) and compared to cougar kill sites prior to wolves (b). Cougar kill sites were compared during summer (S) and winter (W), while the cougar and wolf kill sites were compared only for winter, when wolf predation was primarily sampled, and at two levels: the kill site point (P) and a buffer of 1,260 meters (BF), representing the average distance wolves chased prey on the Greater Yellowstone Northern Range before killing them (Kauffman et al. 2007). A missing letter in the pair indicates that it was not included in top models. While included in top models, the variable roughness is not shown because of scaling issues but is reported in the text. See table 5.5 notes for variables.

than on the higher-elevation, lower-slope-exposure plateaus on the Northern Range. Although elevation and slope were not included in top models, wolves killed prey at higher average elevations and on lesser slopes (2,020 to 2,041 meters and 7- to 8-degree slopes) than did cougars, which killed prey between elevations of 1,926 and 1,968 meters and on 18- to 20-degree slopes. Yet prior to wolf presence, cougars used areas with greater snow depth and that were more similar to areas of wolf kill sites (see fig. 11.13a).

At the kill site and within the chase buffer, odds of cougar kills occurring in cougars' core area were greater than for wolf kills to be in the core area of wolves, probably because core areas provided the most secure habitat for cougars—forested and rough terrain (see chapter 11). These results suggested that wolf kills were more dispersed across the landscape than were cougar kills. To examine this, we tested for a difference in the distribution of cougar- and wolf-killed elk. During early and later wolf restoration periods, cougar kills were more tightly grouped in distribution, or closer to a central x-y location, than were wolf kills [23]. Because wolf packs typically spread out as they foraged across a larger portion of the Northern Range, their kills were indeed more scattered than those of cougars (see also Wilmers et al. 2003b).

### Kill Sites of Cougars before and during Wolf Restoration

Relative to where cougars killed prey in winter prior to wolf presence, cougars killed ungulate prey at greater distances (4 times the odds) from hunting and escape cover once wolves were restored. In the DW study, winter kills of cougars were less likely (3 times less so) to be in areas used by elk and also less likely (almost 2 times less so) to be in areas with increasing snow depth compared to the PW study. Yet overall, the differences in where cougars killed prey during winter were less clear, as indicated by the poor fit of models (table 5.5) [24].

A clearer separation occurred in summer (fig. 5.13b). In the DW study, cougar kills were more likely (3 times) to be farther from hunting and escape cover, less likely (652 times) to be in rough terrain, and less likely (2 times) to be in the core area of cougars compared to kills made by PW cougars. Cougar kills were less likely (8 times) to be in areas increasingly used by elk compared to cougar kill sites prior to wolves. Therefore, results for summer are in contrast to predictions associated with facilitation from wolf predation on elk.

### Kill Sites of Large versus Small Ungulate Prey

The size of ungulate prey had some bearing on where they were killed by cougars, likely influencing many of the preceding results. Large ungulate prey, primarily adult elk, tended to be killed by cougars on less steep slopes, at lower elevations, and farther from escape cover than kills of small ungulate prey (table 5.6) [25]. Such areas had greater use

**TABLE 5.6.** Kill site properties for 426 large ungulate (primarily adult elk) and small ungulate prey killed by cougars during wolf restoration on the Greater Yellowstone Northern Range, 1998–2005. Ranges provided are 95 percent confidence intervals for continuous variables and proportions for noncontinuous variables.

| Variable           | Large Prey Kills            | Small Prey Kills            |
|--------------------|-----------------------------|-----------------------------|
| Elevation          | 1,960 and 2,014 meters      | 2,001 and 2,057 meters      |
| Slope              | 15° to 17°                  | 18° to 20°                  |
| Distance to escape | 20 to 38 meters             | 8 to 16 meters              |
| Forest or open     | 58% open;<br>42% forested   | 49% open;<br>51% forested   |
| Moved to cover     | 33% moved;<br>67% not moved | 54% moved;<br>46% not moved |
| Season             | 26% summer;<br>74% winter   | 38% summer;<br>62% winter   |

by wolves and were also areas where bears readily detected cougar kills. Although a greater proportion of adult elk were killed in open areas (58 percent) compared to forested areas (42 percent), the difference was only marginally significant compared to the proportions of small ungulate prey killed in open (49 percent) and forested areas (51 percent) [26]. Several factors seem apparent in affecting where cougar kills were located. First, cougars were unable to move adult elk to cover for feeding and caching as readily as they could move small ungulate prey, yet large prey killed on greater slopes were sometimes successfully dragged or slid on snow to cover [27]. Second, small ungulate prey killed in the open were closer to forested or rough terrain than were large prey killed in the open (table 5.6). Cougars that killed prey near escape cover and the shorter time required to consume small prey potentially provided enough security for cougars not to feel compelled to move prey into even greater cover.

### INTERACTING FACTORS INFLUENCED PREY SELECTION BY COUGARS AND WOLVES

A review of the diet of cougars and wolves studied in various northern Rocky Mountain ecosystems yields similar proportions and ages (young, prime-age, old) of prey, yet some differences in order of preference of prey (table 5.7). In each study the absolute and relative abundance of prey and prey vulnerability were two of several interacting factors—along with hunting technique and landscape features—that influenced what cougars and wolves selectively killed (see Mech

**TABLE 5.7.** Order of prey selection by cougars and wolves, relative to diet and prey abundance, in four Rocky Mountain study areas, Idaho, Montana, and Wyoming.

| Location                                      | Order of Prey Selection                                     | Study                    |
|-----------------------------------------------|-------------------------------------------------------------|--------------------------|
| NORTH FORK OF FLATHEAD RIVER, MT              |                                                             |                          |
| Cougars                                       | Deer>> Elk>> Moose                                          | Kunkel et al.<br>1999    |
| Wolves                                        | Elk>> Deer>> Moose                                          |                          |
| SALMON RIVER, ID                              |                                                             |                          |
| Cougars                                       | Elk calves>> Cows>> Bulls                                   | Husseman et al.<br>2003b |
| Wolves                                        | Elk calves>> Cows>> Bulls                                   |                          |
| MADISON VALLEY, MT                            |                                                             |                          |
| Cougars                                       | Bull elk>> Female elk; no selection for calves or mule deer | Atwood et al.<br>2009    |
| Wolves                                        | Bull elk>> Female elk; no selection for calves              |                          |
| GREATER YELLOWSTONE NORTHERN RANGE, MT AND WY |                                                             |                          |
| Pre-wolf cougars                              | Elk Calves>>Bucks-Does-Fawns>>Cows-Bulls                    | Murphy 1998              |
| During wolf cougars                           | Elk Calves>>Bucks-Does-Fawns>>Cows-Bulls                    | This study               |
| Wolves                                        | Elk Calves>>Bulls>>Cows                                     | Smith et al. 2004        |

et al. 1995; Kunkel et al. 1999; Pierce et al. 2000a; Husseman et al. 2003b; Murphy and Ruth 2010: 130). In this section we summarize these interacting factors relative to predation on the Greater Yellowstone Northern Range.

### Prey Abundance

On the Northern Range, cougar and wolf preference for calves relative to their availability was strong within and among all years. Elk calves made up a consistent 30 percent to 40 percent of wolf-killed elk and 40 percent to 78 percent of cougar-killed elk. The pattern of selecting calves was also driven by the relative abundance of calves compared to adult elk, with both carnivores killing a greater proportion of adult elk as the ratio of calves to adults declined in the later years of the study and after wolves were colonized (Smith and Bangs 2009). Despite the declining abundance of calves and elk overall, cougars did not switch to other, less abundant prey. Hence the presence and abundance of prey were reflected in the carnivore diet, supporting the prey-abundance hypothesis on a broad scale (Hopcraft et al. 2005).

In the wolf-elk-bison system of the interior Madison-Firehole of Yellowstone, Garrott and colleagues (2009a)

similarly found that wolf predation on bison increased in the later years of the study when bison abundance increased relative to elk. The majority of predation occurred on bison calves but also adults in late winter, when both calves and adults were in their most substandard physiological condition (Becker et al. 2009a). In Banff National Park, Alberta, Kortello and co-workers (2007) supported prey switching as a result of competition for elk, which numbered significantly fewer than the number present in Yellowstone. They found that as cougars and wolves competed for declining numbers of elk, the cougar diet switched to less abundant bighorn sheep and deer. Wolves also switched to less abundant prey, but as the dominant competitor, their change in diet was delayed relative to that of cougars.

### **Prey Condition and Carnivore Hunting Technique**

Interacting with the relative abundance of calves and adult elk, nutritional condition—particularly of adult elk—and carnivore hunting behavior influenced whether prey ended up in the diet of cougars and wolves during winter. Prey size imposes limits for solitary hunters, and poor prey condition enhanced cougars' opportunity to profit from making a large kill with reduced risk (Murphy 1998). In our study wolf diets generally included a greater proportion of adult elk than did cougar diets, but contrary to predictions, we found little disparity in the condition of adult cow elk killed by cougars and wolves. As winter progressed, both carnivores increasingly killed calves and adult elk that were unlikely to survive the winter, probably as a result of the rising availability of nutritionally compromised elk across the landscape (see figs. 7.7 and 7.8). Similar to wolf selection of adult elk, weakness because of injuries, parasites, or disease may also enable cougar predation on large adult prey.

Bull elk were particularly formidable prey, and cougars did not kill bulls until late winter. Even then, only those in poor condition showed up as prey (Murphy and Ruth 2010). Wolves likewise killed few bull elk early in the winter, generally focusing on calves and old cows (Smith and Bangs 2009). An extended drought of more than ten years may also have reduced the quantity and quality of forage for elk, thus affecting the condition of cows, calves, and bulls as they entered winter (Smith and Bangs 2009). Such effects were likely most acute for bull elk because of the demands for peak body condition prior to the rut. Entering the rut in less

than optimal condition in concert with deepening snows as winter progressed translated to bulls being particularly vulnerable to wolf predation, and wolf prey selection changed accordingly. As winter progressed, cows also experienced increased energetic demands because they were at or nearing parturition. Cougars killed cow elk in poor condition in proportion to their expected availability, whereas wolves killed more cows in poor condition than their expected availability would indicate, supporting wolves' selection for compromised cows.

Compared to the wolf literature, there is meager quantitative information on the condition of cougar-killed prey for comparisons. In his central Idaho wilderness study, Hornocker (1970) was the first to report that 63 percent of elk calves, 36 percent of yearling and adult elk, 46 percent of deer fawns, and 46 percent of adult deer killed by cougars were in poor physical condition, with femur marrow less than 50 percent. Among smaller prey, cougars and wolves may differ little in terms of the size, age, or condition of prey they kill because the relatively small size of these prey makes them more equally vulnerable to predation (Murphy 1998). In our PW and DW studies, cougars showed little difference in selection of fawns, does, and bucks. Similarly, in and near Glacier National Park, Kunkel and colleagues (1999) reported that cougars and wolves killed deer of similar age, sex, and condition.

Although greater differential prey selection between wolves and cougars may occur in multi-prey systems where elk are more abundant than deer (Kunkel et al. 1999), we expected few differences in the condition of calves killed by the two predators because of the calves' smaller size. In contrast to our prediction, the femur marrow fat of wolf-killed calves averaged 13 percent less than that of cougar-killed calves, indicating that wolves selected for vulnerable calves more than cougars did on the Northern Range. In studies in eastern Idaho and the Madison Range, Montana, predictions also held during winter—compared to wolves, cougars killed fewer large and compromised prey (Husseman et al. 2003b; Atwood et al. 2007). In Idaho, Husseman and colleagues (2003b) reported that wolves killed elk and mule deer with femur marrow fat averaging 14 percent and 17 percent less, respectively, than in elk and deer killed by cougars. Similarly, femur marrow fat of wolf-killed adult elk in the Madison Range, Montana, averaged 21 percent less than in cougar-killed adult elk (Atwood et al. 2007).

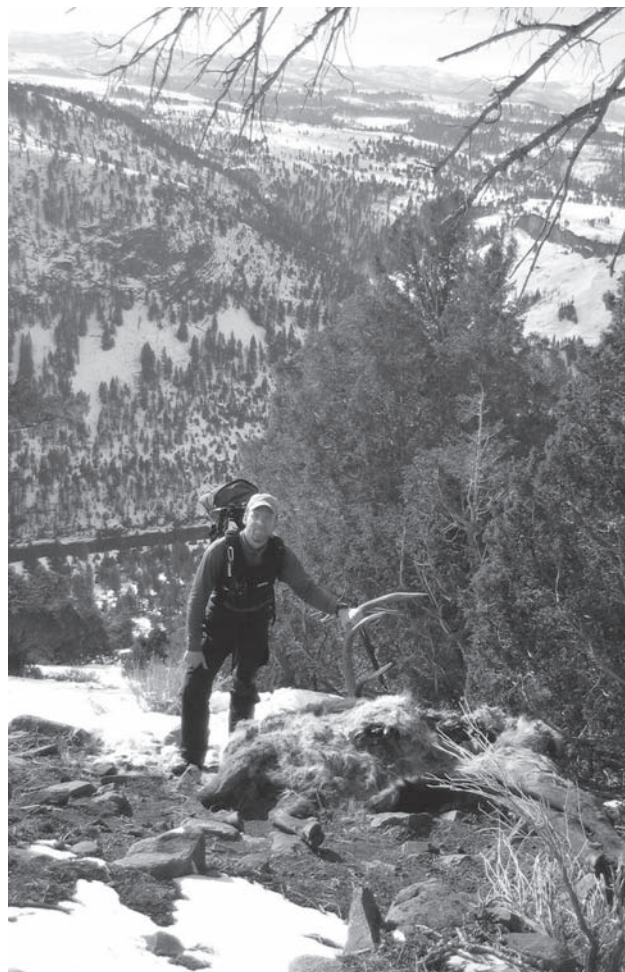


### Landscape Features and Predation Facilitation

Cougar spatial-habitat response to increasing wolf density, discussed in subsequent chapters, and landscape features also explained differences in prey selection of cougars and wolves. In our DW study, cougars were most successful killing prey in habitats that supported less elk use than their PW counterparts, while wolves successfully killed elk in areas that averaged three times greater elk use. Cougars may be successful hunting in areas with lower densities of prey because those areas still offer opportunities for success as related to habitat structure (see chapter 10; Murray et al. 1994; Durant 1998).

During winter, groups of elk—much smaller than those observed on the large open plateaus—moved along trails and accessed small isolated patches of grass on south-facing slopes containing less snow, which were interspersed within forested and rugged terrain. In particular, elk used one such trail situated at roughly 2,300 to 2,400 meters (7,600–7,900 feet) and which, because of heavy use, allowed access through deeper snow. This trail enabled elk to access the area and then disperse onto lower south-facing slopes to forage at 1,680–1,980 meters (5,500 to 6,500 feet). We used this trail, too, as one of our main access points to all areas north of the Yellowstone River between Jardine, Montana, and Hellroaring Creek in Yellowstone. Although we encountered occasional use by wolves—primarily as an efficient travel route and occasionally for hunting—adjacent landscape features provided advantages to cougars (fig. 5.14). The rugged terrain and timber may not only have hampered escape of prey under attack; it may also have meant cougars were able to conceal prey and escape from competitors more effectively in dense vegetation and rough terrain. Other studies support this ambush-habitat hypothesis, where predators benefit by hunting in areas where prey are locally scarce, over the prey-abundance hypothesis, which may enhance prey selection and catchability for coursing predators (Hopcraft et al. 2005). One example comes from the Serengeti, where while avoiding lions and hyenas, Serengeti cheetahs apparently benefited from concentrating on areas with low densities of gazelles. Gazelles in these areas had a lower mean group size and were less likely to detect a hunting cheetah (FitzGibbon 1990; Durant 1998).

In multiple-predator systems, habitat selection by herbivores often reflects a balance between the marginal fitness gain as a result of improved access to forage and the mar-



**FIGURE 5.14.** Troy Davis, Yellowstone National Park biologist, helps collect data from a bull elk killed by female cougar F107 on the south-facing slopes above the Yellowstone River and below a frequently used wildlife trail. During winter, cougars were often successful at killing elk near this trail. Photo by Toni Ruth, Hornocker Wildlife Institute/Wildlife Conservation Society.

ginal loss of fitness as a result of predators (Fortin et al. 2005). This balancing act implies that, at times, elk might have used localized areas of their environment differently in response to predation pressure from coursing wolves or stalking cougars. Hence at localized areas and times, wolves might have facilitated predation by cougars on the Greater Yellowstone Northern Range. Research in Glacier National Park and the Madison Valley, Montana, supports this notion: prey made temporary shifts away from high wolf use areas to structurally complex and dense habitats



(Kunkel 1997; Atwood et al. 2009). In the Madison Valley study, Atwood and co-workers (2007, 2009) concluded that wolves did facilitate cougar predation on elk, which in turn appeared to dilute the risk of predation for mule deer.

There are several reasons why we do not think predation facilitation by wolves occurred consistently during our studies. First, although wolves preferred using areas with higher densities of elk, elk appeared to be astute at assessing the degree of risk associated with intensity of wolf use. Elk did not avoid areas frequented by wolves except at the very highest levels of wolf use (Kunkel and Pletscher 2001; Fortin et al. 2005; Bergman et al. 2006). This meant that elk continued to access high-quality forage, although wolves also selected for those areas (Mao et al. 2005; Bergman et al. 2006; Kauffman et al. 2007; White et al. 2009b). Elk apparently mediated risk of predation from wolves through small-scale movements, increased grouping behavior, or use of particular landscape features—open patches devoid of snow—that provided effective escape (Mao et al. 2005; Bergman et al. 2006; Kauffman et al. 2007; White et al. 2009c). When traveling in areas of high wolf use, which cougars typically avoided, elk did prefer to travel through coniferous forests, but the presence of steep slopes (slopes ~65 degrees) impeded elk movement (Fortin et al. 2005). Further, there was little support for changes in the types of habitats where wolves killed elk over ten years after restoration, an expected response if elk altered their habitat selection and movement patterns to avoid encountering and being killed by wolves (Kauffman et al. 2007).

Second, contrary to our predictions, during periods of wolf restoration, cougars killed prey farther from forested and rugged terrain and outside the most secure part of their home range (the core area) more than did their PW counterparts. Another possibly interacting component is that as calves became less available, cougars increased predation on nutritionally compromised adult elk, particularly during winter. Adult elk were more frequently killed by cougars in open habitat on lesser slopes. In combination, the results suggest that cougars potentially took greater risks to hunt prey and were exposed to greater risk of displacement from large prey, which contrasts with predictions of wolves consistently facilitating cougar predation. In subsequent chapters on spatial and habitat use by cougars, where we delve into these hypotheses in greater detail, our analyses revealed that cougars avoided high wolf use areas, strongly so during winter. In avoiding wolves, cougars were unlikely to have

increased access to elk in areas with low to moderate wolf use. Elk were less likely to move into conifers and more likely to use preferred open and aspen foraging sites in areas of lower and moderate wolf use.

Finally, little information exists on how long anti-predator responses are sustained. The decreased use of aspen stands by elk inhabiting risky, high wolf use areas reflects a tradeoff between safety and the search for food. Yet elk and deer must return to high-quality forage and may do so relatively quickly, thus returning to preferred aspen stands or open habitats where detection of predators through grouping should be a more effective anti-predator strategy (White et al. 2003; Fortin et al. 2005). In multi-predator systems prey may more often avoid denser cover, preferring to feed in more open habitats, as good cover and camouflage imposes limits on their ability to use the many eyes of a group to detect danger (Sinclair 1985; Prins and Iason 1989; Sinclair and Arcese 1995; Hopcraft et al. 2005). In the Madison-Firehole of Yellowstone, elk aggregated ephemerally when wolf predation risk was high, and then as the immediate risk subsided they reverted to smaller foraging aggregations similar to when no wolves were present. Such variations in group size may be an effective anti-predator strategy because unpredictable behavior can reduce predator efficiency (Bowyer et al. 1999). Therefore, although elk may occasionally and temporarily shift to habitats that increase their risk of predation from cougars, we did not find strong support for the idea that wolves facilitated predation by cougars. The finer nuances associated with the question of predation facilitation remain ripe for study.

## SUMMARY

Cougars and wolves competed for similar prey—elk calves followed by adult elk. A decline in calf production equated to increased risk of predation for compromised adult elk during winter, yet both carnivores continued to prefer calves relative to their availability. Whereas wolves showed increased preference for bull elk, cougars increased their take of prime-age cow elk—both reproductively important components of the elk population. Even so, some proportion of these carnivore-killed adults was made up of individuals unlikely to have survived winter because of injuries, parasites and disease, and overall poor condition. Wolves dominated in the areas with the greatest use by elk, whereas cougars, by using competition refuges frequented less by elk

### Text Box 5.1. Preference for Pronghorn

While aerially locating F125 for us at the beginning of one kill rate sampling sequence, pilot Doug Chapman observed F125 ambush a female pronghorn at noon on June 1, 2002. As he homed in on F125's radio-collar signal, Doug noticed the pronghorn standing in a large grassy opening near an edge of Douglas-fir trees, her attention clearly focused into the trees. Within seconds, F125 bounded from the trees and killed the female pronghorn. As we investigated the site the following day, we found that female cougar F125 had dragged the pronghorn almost 200 meters through the grassy sage-steppe to a cliff edge before feeding with her three kittens of the year. While we continued to follow F125 for kill rate sampling from June 1 through June 27, 2001, she killed in sequence a total of four pronghorn and four elk—not including young in utero—during six predation events (table 5.8). Bears displaced F125 from four of these six kills within twenty-four to forty-eight hours. We were unable to track F125 the following summer because of radio-collar failure, but we documented her killing a pronghorn doe on October 24, 2003. Later we re-collared female F125 with a GPS collar, which enabled us to document every kill she made from May 3 through September 27, 2004. During this time, we discovered one adult male pronghorn killed on August 16 and one four- to five-month-old male pronghorn fawn killed on September 21.

**TABLE 5.8.** Prey killed by female cougar F125 during a predation sampling sequence on the Greater Yellowstone Northern Range, June 2002.

| <i>Date</i> | <i>Prey</i>                         | <i>Days<br/>on Kill</i> | <i>Displacement</i> |
|-------------|-------------------------------------|-------------------------|---------------------|
| June 1      | Pronghorn doe with 2 young in utero | 2                       | Grizzly bear        |
| June 5      | Elk calf                            | 4                       | None                |
| June 12     | Pronghorn doe and newborn fawn      | 1                       | Black bear          |
| June 13     | Pronghorn doe                       | <1                      | Unknown bear        |
| June 18     | Cow elk with 1 young in utero       | 1                       | Black bear          |
| June 22     | 2 elk calves                        | 6                       | None                |

(see also chapters 10 and 11), were successful because these habitats enabled catchability of prey for cougars.

More difficult to tease out of the prey selection findings is how the presence of a dominant carnivore influenced the subordinate competitor's access to prey as well as the types of habitat in which cougars chose to hunt to reduce interference competition. In subsequent chapters we present our findings that cougars were better able to conceal kills in more forested and rugged terrain (chapter 7) and that they clearly avoided areas with high wolf use, particularly during winter. As we elaborate further in chapters 10 and 11, we found little evidence that wolf presence facilitated cougar predation on elk.

## CHAPTER 6

### Rates of Predation

#### CONTRIBUTING AUTHORS

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In the few systems where both cougars and wolves were present, their influence on prey has been examined primarily through comparisons of patterns of prey selection (Kunkel et al. 1999; Husseman et al. 2003b; Atwood et al. 2007). Such comparisons, while important to understanding prey vulnerability to each carnivore as well as how predation influences different species and sex-age classes of prey, did not reveal how frequently each carnivore must kill, factors influencing kill rates, or the combined predatory influences of cougars and wolves on prey (but see Husseman 2002). Calculating this *total predation rate* requires (1) knowledge of the rate at which individuals, social classes, or groups of carnivores make kills and (2) an estimate of how many carnivores in each class or group reside within a given area of interest (Holling 1959; Taylor 1984; Murphy 1998; Murphy and Ruth 2010). Although these two basic components of predation are typically of interest to biologists and agency managers, they are not always easily obtained. Our study was distinctive in that Murphy (1998) determined cougar kill rates and factors that influenced how frequently the cats killed prior to wolf restoration. In addition, during wolf restoration, both our study and the Yellowstone Wolf Project were working in tandem to document rates of predation of cougars and wolves. Although kleptoparasitism by bears did not substantially alter predation rates of cougars prior to wolf restoration in our study area (see Murphy 1998; Murphy et al. 1998), with the return of wolves we expected the kill rate of subordinate cougars to be influenced by exploitation and interference competition from wolves and bears.

In this chapter we address four key questions: (1) Did cougars kill at a greater frequency during wolf restoration compared to PW kill rates? (2) Do cougars target vulnera-

ble prey, as wolves do? (3) What factors, such as prey size or displacement by other carnivores, influenced kill rates of cougars and wolves? And (4) do wolves kill at an appreciably higher rate than cougars? In chapter 8 we combine this information with that presented in chapters 5 (prey selection) and 7 (kill displacement) to assess the combined influence of cougars and wolves on prey.

#### DETERMINING KILL RATES OF COUGARS

We determined the kill rate of cougars by sampling randomly from radio-collared cougars and stratifying by social class (chapter 3; Murphy 1998). Prior to the return of wolves, we radio-marked an estimated 77 percent of adult cougars present on the study area by winter 1988–89, with 87–94 percent radio-marked in all subsequent years of the study. During wolf presence we radio-marked an estimated 68 percent and 88 percent of adult cougars present on the study by winters 2000–2001 and 2001–2, respectively, with 88–93 percent radio-marked in all subsequent years until the final year of study (Ruth et al. 2011). The adult study population remained relatively stable in the DW study phase; therefore we sampled with replacement, although individuals were only available for resampling in different seasons and different social classes (Ruth et al. 2010). For example, if we conducted a predation sequence on a solitary adult female cougar during winter, she was available for resampling only as a maternal female or in summer.

Before wolves were returned to the ecosystem, cougars were collared with VHF radio collars and were often located only once a day and usually diurnally (Murphy 1998). Our DW study initially employed the same VHF methods, but later we also utilized GPS technology to increase sample sizes and quantify bias associated with daytime-limited

VHF predation sequences (Ruth et al. 2010). Spatially clustered locations formed where an individual cougar localized, and by downloading data from the GPS collar, these clusters were detected and then searched for kills (Anderson and Lindzey 2003; Sand et al. 2005; Ruth et al. 2010). While ground-telemetry and GPS methods introduced different sources of bias, they yielded similar estimates of cougar kill rates for each adult social class (see Ruth et al. 2010). As a result, we used both VHF and GPS information when comparing cougar kill rates during wolf restoration to pre-wolf kill rates and to kill rates of wolves.

During wolf restoration we followed radio-collared cougars to determine kill rate for approximately 15 percent to 100 percent of the time during each summer and approximately 18 percent to 77 percent of the time during each winter. Some of our sampling efforts were influenced by GPS collar malfunctions, and we were able to sample only one maternal female with GPS methods. Otherwise, we sampled equally with our VHF and GPS methods within each social class: three to five individuals with VHF and three to five individuals with GPS methods (Ruth et al. 2010). We assigned each kill event either to winter (November 1 through April 30) or summer (May 1 through October 31), using an estimated date of death for kills or the first GPS location in a cluster.

Prior to wolf restoration (1990–95), Murphy (1998) completed 24 predation sequences on 20 individual cougars—11 resident adults and 9 independent subadults. These predation sequences lasted an average of 31 days (range = 16–55 days), during which an average of 3.5 kills (range = 2–6) were documented per sequence. During wolf restoration, between November 16, 1998, and June 25, 2005, we conducted 16 VHF and 21 GPS predation sequences on 11 resident adults and 5 independent subadults (Ruth et al. 2010). Our kill rate sampling of cougars in the DW study continued for an average of 30.4 days (range = 17–68 days) for VHF predation sequences and 38.1 days (range = 5–194 days) for GPS predation sequences, during which we documented an average of 5.2 kills (range = 0–36 kills) per sequence.

After the arrival of wolves, we searched 382 VHF predation locations, which included 165 locations associated with 53 kills (12 large prey, 41 small prey), 152 bed sites, and 65 locations with other sign (e.g., tracks) or with no obvious cougar sign. We also visited 196 GPS location clusters (average of 10 locations/cluster, SD = 10.5), at which we documented 142

kills (58 large prey, 80 small prey, 4 undetermined prey size), 32 bed sites, and 22 sites with other sign or with no obvious cougar sign (Ruth et al. 2010). Time records from GPS collars revealed that cougars made most kills during crepuscular hours and at night, primarily between 2000 and 0500 hours (Ruth et al. 2010). After the cougar left we searched sites where we located cougars for 10 minutes to 11 hours (average of 1.5 hr, SD = 1.4 hr), with cluster sites searched the longest and on multiple days (fig. 6.1).

We used two methods to estimate *individual kill rates* of cougars (Murphy 1998; Ruth and Murphy 2010a). We used Murphy's (1998) inter-kill interval method to make consistent kill rate comparisons between PW and DW periods using statistical analyses. This estimate resulted from taking the total number of days, including the first day the focal cat was at a kill, through the day before the last kill in the documented sequence and dividing by the number of kills, including the first but excluding the last kill. Although we predicted an increase in kill rate in the DW study, we conducted two-sided tests to detect changes in either direction, with an alternative hypothesis being that exploitative competition with wolves for space and prey could reduce cougar access to prey and thus their encounter rate with prey, resulting in a lower kill rate.

We used a second method—the ratio estimator (Hebblewhite et al. 2003)—to make comparisons between cougar and wolf predation because it was similar to methods used by Smith and co-workers (2004) to determine wolf kill rates. It also allowed for comparison to cougar kill rates calculated by Knopff and colleagues (2010b) in a cougar-wolf system in Canada. For this method we used the total time we monitored a focal cougar and the total number of kills documented during that time.

Compared to the PW study, we sampled fewer subadult cougars (five total) during wolf restoration, as few subadults remained in the study area long enough to sample after separating from their mothers. We further noted that subadult cougars tended to spend a longer time between making ungulate kills (an average of between 7.5 and 19.2 days) than adult cougars. Yet subadults consumed carcasses more completely (70 percent to 90 percent) than did adults, except for maternal females with yearling offspring (Murphy 1998). Some subadult males appeared to remain at a carcass well after it was consumed to maintain a low profile while wedged in between adult male home





**FIGURE 6.1.** Handheld GPS units helped Toni Ruth navigate to search a cluster of cougar locations for a kill and other carnivore sign. Wildlife Conservation Society photo.

ranges during winter. Two examples of subadult behavior documented during our kill rate sampling are provided in text box 6.1. As a result of fewer subadults sampled, we compared kill rates only of resident adults between PW and DW study periods. Because wolf packs were made up of adults, subadults, and pups, we included solitary and maternal adult cougars as well as subadults when making comparisons to wolf kill rates.

#### **RATE OF FOOD ACQUISITION BY COUGARS**

After we excluded subadults from our calculations, sampling to document kill rate resulted in 39 kill intervals from eleven adult cougars in the three adult social classes prior to wolves, 1990–95 (table 6.1; Murphy 1998). During wolf presence (1998–2005) we sampled eleven adult cougars and documented 113 kill intervals. As a result, we sampled

kill rate on 100 percent and 80 percent of the average estimated adult population prior to and during wolf restoration, respectively.

#### **Average Kill Rates of All Cougars**

Adult cougars killed prey at a slightly increased rate during wolf presence (7.0 days/kill) as compared to the PW period (7.9 days/kill), although the difference was not significant, running contrary to our predictions (table 6.1) [1]. We obtained a greater number of kill intervals for DW cougars, yet across all months the frequency at which cougars killed was quite similar during the two study periods (fig. 6.2). At first glance this suggests that the frequency at which cougars killed prey was not appreciably increased by competition with wolves, the increasing number of grizzly bears, or declines in elk that occurred over the DW study.

**TABLE 6.1.** Mean and median kill rate of adult cougars prior to wolves (1990–95) and during wolf restoration (1998–2005) on the Greater Yellowstone Northern Range. Days per ungulate kill and kilograms of biomass per day were calculated using the inter-kill interval method, standard error (SE), and lower and upper 95 percent confidence intervals (LCI, UCI). Sample size, *n*, indicates number of inter-kill intervals, measured as days between successive ungulate kills, followed by the number of cougars sampled (in parentheses).

| Study Phase and Social Class | Days/Kill Estimate    |      |     |     |      |        | Kg/Day Estimate |      |     |      |      |        |
|------------------------------|-----------------------|------|-----|-----|------|--------|-----------------|------|-----|------|------|--------|
|                              | <i>n</i> <sup>a</sup> | Mean | SE  | LCI | UCI  | Median | <i>n</i>        | Mean | SE  | LCI  | UCI  | Median |
| <b>PRE-WOLF</b>              |                       |      |     |     |      |        |                 |      |     |      |      |        |
| Adult females                | 9(4)                  | 11.3 | 1.7 | 7.9 | 14.7 | 12.0   | 9(4)            | 10.5 | 2.4 | 5.9  | 15.1 | 6.9    |
| Adult males                  | 16(3)                 | 7.3  | 1.1 | 5.2 | 9.4  | 6.5    | 16(3)           | 30.8 | 8.0 | 15.1 | 46.5 | 13.5   |
| Maternal females             | 14(4)                 | 6.5  | 0.7 | 5.1 | 7.9  | 7.5    | 14(3)           | 20.1 | 6.0 | 8.4  | 31.8 | 17.0   |
| All adults                   |                       | 7.9  | 0.8 | 6.4 | 9.4  | 8.0    |                 | 22.3 | 3.7 | 15.1 | 29.5 | 13.5   |
| <b>DURING WOLF</b>           |                       |      |     |     |      |        |                 |      |     |      |      |        |
| Adult females                | 28(6)                 | 9.8  | 1.0 | 7.8 | 11.8 | 8.5    | 25(6)           | 19.1 | 3.6 | 12.0 | 26.2 | 14.4   |
| Adult males                  | 23(4)                 | 7.3  | 0.7 | 6.0 | 8.6  | 7.0    | 22(4)           | 25.8 | 4.8 | 16.4 | 35.2 | 20.1   |
| Maternal females             | 62(5)                 | 5.4  | 0.4 | 4.6 | 6.2  | 5.0    | 57(5)           | 26.7 | 3.2 | 20.5 | 32.9 | 15.8   |
| All adults                   |                       | 7.0  | 0.4 | 6.2 | 7.8  | 6.0    |                 | 24.6 | 2.1 | 20.4 | 28.8 | 15.5   |

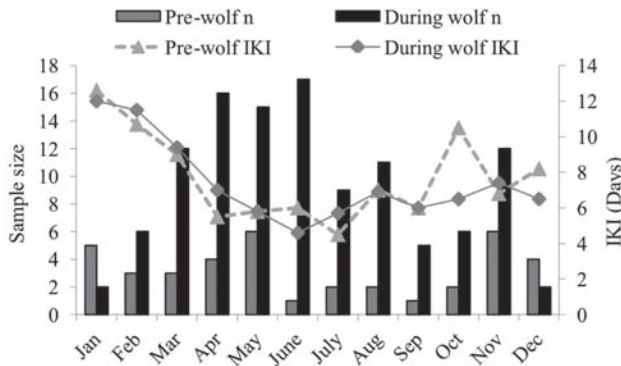
<sup>a</sup> We conducted PW kill rate sampling sequences for eleven adult cougars, 1987–94, and during wolf sampling for eleven adult cougars, 1998–2005. During wolf sample sizes are greater than eleven individuals because we sampled with replacement; thus some female cougars were sampled in both the adult and maternal female categories.

The frequency at which cougars killed ungulate prey was influenced by factors that could be masked when simply looking at the frequency at which they kill. These include: (1) the size of prey, (2) the number and size of cougars feeding at a kill, (3) the gender, age, and reproductive status of cougars, and (4) the frequency and degree to which kills were kleptoparasitized by competitors (Murphy 1998; Anderson and Lindzey 2003; Knopff et al. 2010b; Ruth et al. 2010). Hence we incorporated these factors in our comparisons of PW and DW kill rates and when comparing kill rates of cougars to wolves.

The biomass of meat associated with large ungulate prey sustained an individual or family group of cougars for much longer than small ungulate prey, lengthening the time before the cats killed again (fig 6.3; Murphy 1998; Cavalcanti and Gese 2010). Cougars spent 2.8 to 5.7 days (95 percent confidence interval) feeding on adult and yearling elk and 2.3 to 3.6 days (95 percent confidence interval) consuming small ungulate prey when not displaced by wolves or bears [2].

Cougar kill rates were also constrained by the gender, number, and size of cougars feeding at a kill, with cougar body mass a significant predictor of the kilograms killed by cougars per day (kg/day; Murphy 1998; Knopff et al. 2010b). Because maternal females supported one to four offspring with each kill, when we incorporated biomass of cou-

gars—in addition to the biomass of prey—and standardized the kill rates, we found a clearer picture than that provided with kills per day per cougar (fig. 6.4). Consequently, we incorporated both the biomass of prey and the biomass of cougars into calculations, and we standardized kill rates to kilograms of prey killed per day per cougar (kg/day/cougar) and kilograms of prey per day per kilogram of cougar (kg/day/kg of cougar) to make comparisons between our two study periods as well as to kill rates of wolves (Murphy 1998). To accomplish this, we used age-season growth models developed by Murphy (1998) to estimate the live biomass of each prey killed by cougars or wolves during a given time period such as summer, winter, or the rut. We estimated the mass of cougars based on their weight at capture closest to when we conducted a predation sequence, while the biomass of wolves was calculated as the mean mass of adults or pups when they were weighed in winter (Smith et al. 2004; Metz et al. 2011). We weighed cougar kittens during capture at dens or subsequent captures as they aged—generally at three to six months of age and again as subadults. We estimated kitten mass between measurements using projections of growth per period. We then estimated mass of family groups by adding the actual or estimated weight of kittens to the capture weight of their mother. Our estimation of kill rates did not account for inedible portions of the prey such

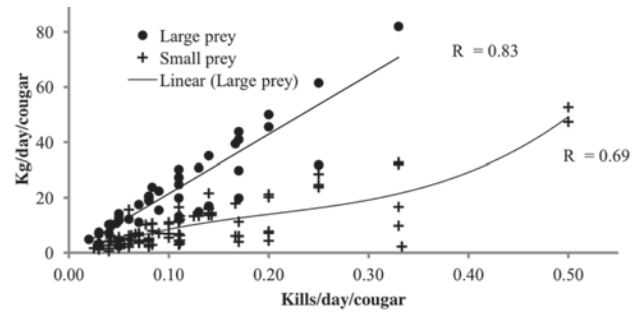


**FIGURE 6.2.** Number of ungulate kills per day (IKI days) and inter-kill intervals (sample size) for adult cougars before and during wolf restoration on the Greater Yellowstone Northern Range, Montana and Wyoming. We conducted PW kill rate sampling sequences for eleven adult cougars, 1987–94, and DW sampling for eleven adult cougars, 1998–2005.

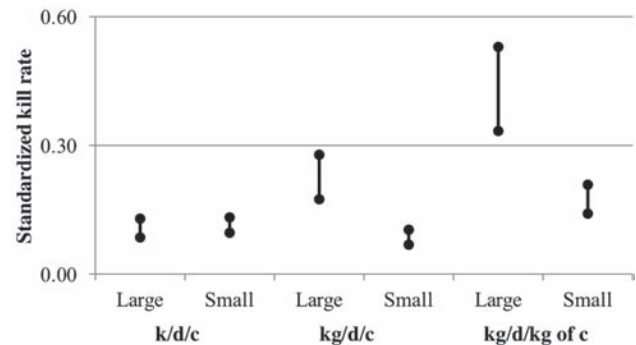
as bones, stomach, and intestines, as these varied with prey size. We also did not adjust for actual consumption, which varied when cougars were displaced from or simply abandoned carcasses. Retaining information on displacements was important, as we were interested in how displacement from kills affected kill rates after wolf restoration.

### Average Kill Rates of Cougar Social Classes within Study Phase

When we compared across cougar social classes within each study phase, the frequency at which cougars killed prey differed by social class (table 6.1) [3]. In both study phases, females supporting dependent offspring killed more frequently—lowest number of days between consecutive kills, at 4.6 to 7.9 days per kill—and solitary adult females killed the least frequently. This pattern held when we incorporated the biomass of the kill into kill rates, although the difference among social classes was not significant for DW cougars (table 6.1) [4]. One difference between the study periods was apparent in that PW adult males killed prey at a frequency similar to that of PW maternal females. But during wolf presence, adult males killed less often than did DW maternal females and at a frequency more similar to that of solitary females (table 6.1; Murphy 1998) [5]. As we discuss later, adult males minimized time at kills prior to wolf presence, and PW solitary females spent longer moving between kills than either adult males or maternal females.



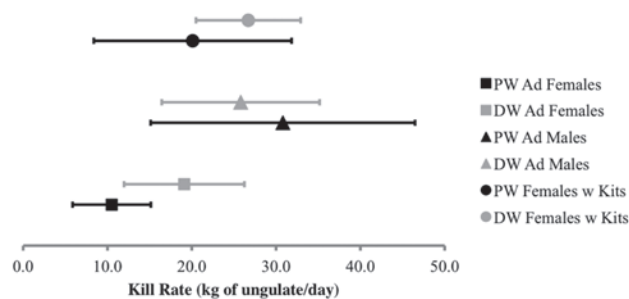
**FIGURE 6.3.** Frequency at which cougars killed ungulate prey (kills per day per cougar) was strongly related to the biomass of prey as incorporated in kill rate (kilograms per day per cougar), particularly with large ungulate prey. A linear relationship provided the best fit for large prey (adult elk), and a polynomial relationship provided the best fit for small ungulate prey (elk calves, mule deer, pronghorn, and bighorn sheep).



**FIGURE 6.4.** Kill metrics that do not account for or standardize by the biomass of prey and predator can provide misleading results in temporal comparisons and comparisons between species or study areas ( $k/d/c$  = kills per day per cougar;  $kg/d/c$  = biomass of prey;  $kg/d/kg$  of  $c$  = biomass of predator).

Although we did not detect a statistical difference during the PW and DW studies in the frequency at which cougars killed prey or in the biomass killed per day, we did notice a trend toward slightly higher kill rates by adult and maternal female cougars after wolf restoration (table 6.1, fig. 6.5) [6]. The lack of support for increased kill rates across all sampled cougars was not expected, and later we revisit the influence of displacement and prey size on kill rates relative to two primary behaviors that comprise the kill interval—*handling time* and *search-hunting time*.





**FIGURE 6.5.** Kill rate in kilograms of ungulate biomass per day of pre-wolf (black) and during wolf (gray) female cougars with kittens (circles), adult males (triangles), and solitary females (squares). Bars are 95 percent confidence intervals around the average.

### WHAT INFLUENCED KILL RATES OF COUGARS?

Although PW and DW cougars killed prey at fairly consistent rates, we needed to gain an understanding of what factors explained variation in the kill rates during the PW and DW studies. To evaluate the characteristics that might explain variation in kill rates of PW and DW cougars, we used multiple regression with the log transformed kill rate standardized to kilograms of prey per day per kilogram of cougar ( $\log$  of kg of prey/day/kg of cougar) as the dependent variable [7]. We added to the prey weight, social class, and ambient temperature factors evaluated by Murphy (1998) and considered thirteen variables in total when developing separate sets of twenty and twenty-eight a priori models for PW and DW studies, respectively (table 6.2). To compare models and determine which provided the best support of the data, we used Akaike's information criterion corrected for small sample size and model weights, as described in appendix B (Burnham and Anderson 2002). We first evaluated multicollinearity and did not include variables that were correlated within the same model (appendix B; Hair et al. 2006; Zuur et al. 2007, 2009).

Prior to wolf restoration, the weight of a prey item, total biomass of elk calves, and intraspecific social forces (indexed by the density of adult male cougars) had the greatest influence on cougar kill rates, explaining 13 percent to 19 percent of variation in kill rates (table 6.3). Not surprisingly, larger ungulate prey translated to higher kilograms of ungulate prey killed per day—kill rate increased by 47 percent with a 100 kg increase in prey weight (table 6.4). During wolf resto-

ration and colonization, the weight (biomass) of a prey item, displacements by wolves and bears, and cougar social class explained 58 percent to 61 percent of the variation in cougar kill rates (table 6.5). Again, larger ungulate prey translated to higher mass of ungulate prey killed per day—kill rate increased by 54 percent with a 100 kg increase in prey weight (table 6.6). The trend toward higher kill rates of DW cougars was related to a greater proportion of large prey available to and killed by cougars relative to elk calves, as well as a greater number of displacements that occurred during wolf restoration.

### Displacements

Prior to wolf restoration, cougars were infrequently displaced from their kills by bears and coyotes. Although cougars lost some biomass of a kill to other carnivores, their kill rate did not increase noticeably as a result of displacements (tables 6.3 and 6.4; Murphy 1998; Murphy et al. 1998). As predicted, this changed as wolves became established in the study area and bear numbers increased. In addition to the weight of killed prey, DW cougar kill rates increased 15 percent to 68 percent when a cougar was displaced from its kill by a wolf or a bear (tables 6.5 and 6.6). When cougars were displaced by another carnivore, their kill rates also varied to a much greater degree (variance = 0.68) than the kill rates associated with no displacements (variance = 0.46) by other carnivores. Wolf and bear detection of cougar kills and displacement of cougars from kills were influenced by the size of prey and by features of the landscape, which became clearer in separate analyses we present later.

Considering influences of displacements and prey size revealed here and the lack of differences in kill rates we found earlier, we broke down that kill rate into its two components—*handling time* and *search-hunting time* prior to making the next kill. Once a kill was made, cougars spent bouts of time feeding at the kill interspersed with bouts of resting away from the cached carcass, resulting in handling times averaging 2 to 3 days (95 percent confidence interval, range = 0.3 to 11 days for our study; Beier et al. 1995; Bank and Franklin 1998; Murphy and Ruth 2010). Following consumption, Greater Yellowstone Northern Range cougars moved on and spent approximately 3 to 7 days (95 percent confidence interval, range 0–18 days) in other behaviors—such as traveling to new areas, searching for mates and marking territories, resting in day beds, nursing kittens, and hunting—



**TABLE 6.2.** Predictions (P) resulting from the hypothesis that variation in cougar kill rates is influenced by competitor use of the landscape (wolves), cougar social class, characteristics of the landscape, seasonal differences, availability of elk and elk calves, prey size, social stability as indexed by the density of male cougars, and the frequency at which cougars are displaced from their kills. See appendix E for descriptions of data. We developed separate sets of a priori models that differed somewhat as hypotheses of factors explaining variation in cougar kill rates prior to and during wolf restoration on the Greater Yellowstone Northern Range, 1987–2005.

| <i>Independent Variable</i>                                          | <i>Rationale and Predictions</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          | <i>References</i>                                      |
|----------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------|
| Prey weight (PreyWt) in kilograms                                    | Large kills provide a greater amount of usable biomass to cougars, and handling time is greater with large kills. Also see predictions in table 7.1.<br>P <sub>1</sub> : Kill rates measured as days/ungulate kill should be lower with increasing prey weight.<br>P <sub>2</sub> : Alternatively, kill rate measured as kg of prey killed/day are higher with increasing prey weight (i.e., greater kg/day averaged over the kill interval than with smaller prey).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      | Murphy 1998; Knopff et al. 2010b                       |
| Social class (Social)                                                | Kill rates vary by social class.<br>Prediction: Maternal females supporting dependent offspring have higher rates of predation than adult males or solitary females.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      | Murphy 1998                                            |
| Winter                                                               | Overlap, and presumably encounter rates, with prey are greater during winter; thus as winter progresses, prey vulnerability increases as condition declines. Detection of cougar kills increases during winter overlap with wolves (also see table 7.1.).<br>Prediction: Cougar kill rates are greater in winter than in summer.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          | Murphy 1998; Ruth 2004a                                |
| Wolf use (Wolfuse) and wolf population (Wolfpop)                     | Wolves dominate cougars at, and displace them from, their kills. Wolf detection of cougar kills is greater in areas with high wolf use and as wolf population numbers increased (i.e., more wolves on the landscape in the same area).<br>P <sub>1</sub> : Cougar kill rates increase as wolf use and numbers increase.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   | Ruth 2004a; Kortello et al. 2007                       |
| Elk population (Elkpop) and calf biomass (Calfbio)                   | Encounter rates with primary prey increase as the numbers of elk and the biomass of calves increase and decline at lower numbers of elk and lower calf biomass. Exploitative competition with wolves for space and prey could reduce cougar access to, and thus their encounter rate with, prey, resulting in a lower kill rate. Dominant competitors also more frequently encounter prey at high elk and calf numbers, which in turn moderates the rate at which they seek out and scavenge carrion.<br>P <sub>1</sub> : Pre-wolf cougar kill rates increase with increasing numbers of elk and calves.<br>P <sub>2</sub> : Cougar kill rates increase with declining numbers of elk and declining calf biomass as displacements by competitors increase.<br>P <sub>3</sub> : Cougar kill rates decline with declining numbers of elk and declining calf biomass, as cougars invest more time to search for prey before successfully killing. Hence, a significant lengthening in the average number of days between kills should occur. | Creel and Creel 2002                                   |
| Displacement (Disp)                                                  | Cougars displaced from kills by wolves or bears compensate for losses in food intake and kill more frequently.<br>P <sub>1</sub> : Kill rates increase following kleptoparasitism by wolves and bears.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    | Harrison 1990; Murphy 1998; Ruth 2004a                 |
| Elevation (Elev)                                                     | Spoilage of cougar kills and losses to microbes are positively related to higher temperatures at lower elevations. Cougars are prone to greater displacement by competitors as a result of dispersion of odor associated with carcasses. Also see table 7.1.<br>P <sub>1</sub> : Elevation and kill rates are inversely related because of greater carcass spoilage and displacements at lower elevations.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                | Mattson et al. 2007; Bischoff-Mattson and Mattson 2009 |
| Forested                                                             | See table 7.1 for rationale and predictions.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |                                                        |
| Cougar density (Cougden) and adult male density (Amden) <sup>a</sup> | To maximize pursuit of mates and discourage incursions of breeding competitors, resident males may take the largest prey but minimize time feeding by gorging or consuming prey incompletely. Whether social relationships are relatively unstable as a population increases or are more stable once individuals are well established and thus familiar with conspecifics could influence the time certain social classes spend on a kill gaining energy versus time spent searching for mates and discouraging incursions of conspecific competitors. Total cougar and adult male densities were used as an index of stability of social relationships.<br>P <sub>1</sub> : Densities and kill rates are inversely related as adult cougars minimize time consuming kills and maximize social interactions at low densities, while adult cougars should spend more time feeding at kills and similar or less time in social interactions at higher densities, reflecting social stability in our study area.                             | Murphy 1998; Mattson et al. 2007                       |

*continued on next page*

TABLE 6.2.—continued

| Independent Variable                          | Rationale and Predictions                                                                                                                                                                                                                                                                                                                                                                            | References  |
|-----------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------|
| Ambient temperature (Temp) in degrees Celsius | As temperatures decline below a critical threshold, cougars may kill more frequently to compensate for extra costs of thermoregulation or, in other words, to keep warm relative to declining temperatures. Increased availability of small prey during warm summer temperatures may lengthen the frequency at which cougars kill ungulate prey.<br>P1: Kill rates increase as temperatures decline. | Murphy 1998 |

<sup>a</sup> We added cougar density and density of adult males into models after development and following the differences we detected between the PW and during wolf cougars in handling time and time spent moving to the next kill. Thus models including these terms were added to and run after development of our original model set.

**TABLE 6.3.** Multiple linear regression models of variables explaining variation in kill rates (log of kg of prey/day/kg of cougar) of cougars prior to wolf restoration, 1990–95, on the Greater Yellowstone Northern Range. Darker gray indicates best models.

| Model <sup>a</sup>                                    | AICc  | ΔAICc | K  | w <sub>i</sub> | R <sup>2</sup> <sub>adj</sub> |
|-------------------------------------------------------|-------|-------|----|----------------|-------------------------------|
| 1. PreyWt + Amden + Calfbio                           | 93.1  | 0.0   | 7  | 0.16           | 0.19                          |
| 2. PreyWt + Amden                                     | 93.3  | 0.2   | 6  | 0.14           | 0.16                          |
| 3. PreyWt + Winter                                    | 93.8  | 0.7   | 6  | 0.11           | 0.15                          |
| 4. PreyWt                                             | 93.8  | 0.7   | 5  | 0.11           | 0.13                          |
| 5. PreyWt + Amden + Temp                              | 94.4  | 1.3   | 7  | 0.08           | 0.17                          |
| 6. PreyWt + Cougden                                   | 94.5  | 1.4   | 6  | 0.08           | 0.14                          |
| 7. PreyWt + Amden + Winter                            | 94.7  | 1.6   | 7  | 0.07           | 0.16                          |
| 8. PreyWt + Cougden + Winter                          | 95.7  | 2.6   | 7  | 0.04           | 0.14                          |
| 9. PreyWt + Temp                                      | 96.0  | 2.9   | 6  | 0.04           | 0.10                          |
| 10. Disp + PreyWt                                     | 96.1  | 3.0   | 6  | 0.04           | 0.10                          |
| 11. Cougden                                           | 96.4  | 3.3   | 5  | 0.03           | 0.07                          |
| 12. Intercept only (Null)                             | 97.9  | 4.8   | 4  | 0.01           | —                             |
| 13. Disp + PreyWt + Social + Amden                    | 98.1  | 5.0   | 9  | 0.01           | 0.14                          |
| 14. Elkp                                              | 98.6  | 5.5   | 5  | 0.01           | 0.01                          |
| 15. Disp + PreyWt + Social                            | 99.2  | 6.1   | 8  | 0.01           | 0.09                          |
| 16. Disp + PreyWt + Social + Winter                   | 99.3  | 6.2   | 9  | 0.01           | 0.11                          |
| 17. Disp + PreyWt + Social + Cougden                  | 99.5  | 6.4   | 9  | 0.01           | 0.11                          |
| 18. Disp + PreyWt + Social + Elev                     | 101.3 | 8.2   | 9  | 0.00           | 0.07                          |
| 19. Disp + Social                                     | 103.1 | 10.0  | 7  | 0.00           | 0.04                          |
| 20. Disp + PreyWt + Social + Winter + Elev + Forested | 104.3 | 11.2  | 11 | 0.00           | 0.05                          |

<sup>a</sup> Variables included in models were: PreyWt = kilograms of prey; Amden = density of adult male cougars corresponding with time frame of kill; Winter = season of year coded as 0 for summer (May through October) and 1 for winter (November through April); Temp = ambient temperature in degrees Celsius; Disp = displacement from kill occurred (1) or did not occur (0); Cougden = density of cougars corresponding to the time frame of a kill; Social = adult male, solitary female, or maternal female; Elkp = total abundance of elk corresponding with the time frame of a kill; Elev = elevation at kill site; and Forested = forest cover at kill site (1) or not (0).

**TABLE 6.4.** Model averaged beta estimates and 95 percent confidence intervals from top linear regression models explaining variation in cougar kill rates prior to wolf restoration on the Greater Yellowstone Northern Range, 1990–95.

| Term                        | Beta (95% CI)      | Interpretation                                                   |
|-----------------------------|--------------------|------------------------------------------------------------------|
| Intercept                   | −0.84 (−3.54–1.86) | NA                                                               |
| 100 kg prey weight (PreyWt) | 0.47 (0.03–0.09)   | Kill rate increased by 47% with a 100 kg increase in prey weight |
| Adult male density (Amden)  | −1.07 (−2.55–0.41) | Effect on kill rate was not clear                                |
| Calf biomass (Calfbio)      | 0.07 (−0.07–0.20)  | Effect on kill rate was not clear                                |
| Winter                      | 0.09 (−0.10–0.28)  | Effect on kill rate was not clear                                |
| 10° temperature (Temp)      | 0.01 (−0.02–0.04)  | Effect on kill rate was not clear                                |
| Cougar density (Cougden)    | −0.03 (−0.08–0.04) | Effect on kill rate was not clear                                |

prior to making the next kill of ungulate prey (Murphy and Ruth 2010; Murphy and Ruth 2010).

Perhaps factors that influenced these components of kill rates differed in some important ways between the two study periods, thus masking differences in cougar kill rates. Hence we asked: If cougars were displaced from kills more frequently after wolf restoration, then shouldn't DW cougars (1) spend less time handling kills and (2) also spend less time in search-hunting bouts between kills because they needed to kill again more quickly? The first prediction was not supported. Unexpectedly, PW cougars spent a median of 1 day less feeding at a kill than did cougars after wolf restoration [8]. Our second prediction was supported: DW cougars spent a median of 2 days less moving between kills than did their PW counterparts [9]. These results explained the lack of difference in kill rates between the two study phases,

as they offset each other. Yet because displacements were infrequent prior to wolves, we still lacked an explanation for the contrasting differences in the time cougars spent at kills and moving between kills in the two study periods.

To explore the differences further, we next removed displacements from our DW kill sample. During wolf cougars killed a greater proportion of large prey (35.5 percent of our kill rate sample) than did PW cougars (15.4 percent). These larger kills did take longer for a cougar to handle and consume than smaller kills, as long as the cougar was not displaced from the kill. Hence DW cougars should have spent a period of search and handling time between kills equal to or greater than that of PW cougars. Yet the greater proportion of large prey did not support predictions, as DW cougars still spent a median of 2 days less searching and hunting between kills than did PW cougars [10]. In combination with the best supported models, these results suggested that large prey and displacements explained much of the variation in cougar kill rates during wolf restoration but that other factors, such as intraspecific social influences, likely explained variation in kill rates prior to wolf restoration.

### Intraspecific Social Influences—Energy-Maximizing and Time-Minimizing Strategies

Our study area experienced relatively low turnover of individual cougars as a result of human hunting, such that as cougar density increased, so did stability of home ranges and familiarity between individuals. Inclusion of total density of cougars and adult male cougar density in models revealed that prior to wolf restoration, kilograms of prey killed per day by cougars declined as adult male density increased (table 6.4). Hence cougar social characteristics had a greater influence on PW cougar kill rates, while the interaction between displacements and prey size had an overriding influence on the frequency at which DW cougars killed prey [11]. Because our models explained at best 19 percent of the variation in cougar kill rates, we suspected that PW cougars were meeting their energy requirements, but beyond this there were likely social and individual behaviors that influenced kill rate, which we could not appropriately model. For example, Murphy (1998) found that scrape rate explained most of the variation in cougar kill rates ( $R^2 = 0.43$ ), but when we separated adults from subadults, we found much of the variation ( $R^2 = 0.83$ ) was caused by scraping by subadult males.

If adult males minimize time at kills to maximize pursuit of mates and territory defense, then they should spend less time handling kills and more search-hunting time between kills than other social classes (Mattson et al. 2007). We further expected that this should be more pronounced when *intraspecific* influences were greater than *interspecific* influences. Yet under risk of predation from competitors, cougars might also maximize energy intake and minimize time at a kill under the threat of encountering a competitor. In

**TABLE 6.5.** Multiple linear regression models of variables explaining variation in kill rates (log of kg of prey/day/kg of cougar) of cougars during wolf restoration, 1998–2005, on the Greater Yellowstone Northern Range. Darker gray indicates best models.

| Models <sup>a</sup>                                            | AICc  | $\Delta AICc$ | K  | $w_i$ | $R^2_{adj}$ |
|----------------------------------------------------------------|-------|---------------|----|-------|-------------|
| 1. Disp + PreyWt + Social                                      | 185.9 | 0.0           | 8  | 0.38  | 0.58        |
| 2. Disp + PreyWt + Social + Winter                             | 187.8 | 1.8           | 9  | 0.15  | 0.58        |
| 3. Disp + PreyWt + Social + Wolfuse                            | 188.1 | 2.1           | 9  | 0.13  | 0.58        |
| 4. Disp + PreyWt + Social + Amden                              | 188.2 | 2.3           | 9  | 0.12  | 0.58        |
| 5. Disp + PreyWt + Social + Elev                               | 188.3 | 2.4           | 9  | 0.11  | 0.58        |
| 6. Disp + PreyWt + Social + Elev + Wolfuse                     | 190.4 | 4.4           | 10 | 0.04  | 0.58        |
| 7. Disp + PreyWt + Social + Elev + Wolfuse + Winter            | 191.0 | 5.0           | 11 | 0.03  | 0.58        |
| 8. Disp + PreyWt + Social + Winter + Elev + Forested           | 192.4 | 6.5           | 12 | 0.01  | 0.58        |
| 9. Disp + PreyWt + Social + Elkpop + Wolfpop + Cougden         | 192.7 | 6.8           | 11 | 0.01  | 0.57        |
| 10. Disp + PreyWt + Social + Elev + Elkpop + Wolfpop + Cougden | 195.2 | 9.2           | 12 | 0.00  | 0.57        |
| 11. Disp + PreyWt                                              | 205.6 | 19.6          | 6  | 0.00  | 0.49        |
| 12. Disp + PreyWt + Wolfuse                                    | 207.9 | 21.9          | 7  | 0.00  | 0.48        |
| 13. PreyWt + Winter                                            | 208.8 | 22.9          | 6  | 0.00  | 0.47        |
| 14. PreyWt + Amden                                             | 210.1 | 24.1          | 6  | 0.00  | 0.46        |
| 15. PreyWt + Cougden                                           | 210.1 | 24.1          | 6  | 0.00  | 0.46        |
| 16. PreyWt + Amden + Winter                                    | 211.1 | 25.1          | 7  | 0.00  | 0.46        |
| 17. PreyWt + Cougden + Winter                                  | 211.1 | 25.1          | 7  | 0.00  | 0.46        |
| 18. Disp + PreyWt + Elkpop + Wolfpop + Cougden                 | 211.4 | 25.5          | 9  | 0.00  | 0.47        |
| 19. Disp + Social                                              | 240.7 | 54.8          | 7  | 0.00  | 0.29        |
| 20. Wolfuse                                                    | 273.5 | 87.6          | 5  | 0.00  | 0.02        |

continued on next page

TABLE 6.5.—continued

| Models <sup>a</sup>          | AICc  | ΔAICc | K | w <sub>i</sub> | R <sup>2</sup> <sub>adj</sub> |
|------------------------------|-------|-------|---|----------------|-------------------------------|
| 21. Intercept only (Null)    | 274.4 | 88.4  | 4 | 0.00           | —                             |
| 22. Elkp                     | 275.5 | 89.5  | 5 | 0.00           | 0.00                          |
| 23. Cougden                  | 276.5 | 90.6  | 5 | 0.00           | 0.00                          |
| 24. Wolfpop                  | 276.6 | 90.6  | 5 | 0.00           | 0.00                          |
| 25. Elkp + Cougden           | 276.9 | 90.9  | 6 | 0.00           | 0.00                          |
| 26. Elkp + Wolfpop           | 277.4 | 91.5  | 6 | 0.00           | 0.00                          |
| 27. Wolfpop + Cougden        | 278.8 | 92.8  | 6 | 0.00           | 0.00                          |
| 28. Elkp + Wolfpop + Cougden | 278.9 | 93.0  | 7 | 0.00           | 0.00                          |

<sup>a</sup> Variables included in models were: Disp = displacement from kill occurred (1) or did not occur (0); PreyWt = kilograms of prey; Social = adult male, solitary female, or maternal female; Winter = season of year coded as 0 for summer (May through October) and 1 for winter (November through April); Wolfuse = index of wolf use as described in appendix E; Amden = density of adult male cougars corresponding with time frame of kill; Temp = ambient temperature in degrees Celsius; Cougden = density of cougars corresponding to the time frame of a kill; Elkp = total abundance of elk corresponding with the time frame of a kill; Elev = elevation at kill site; and Forested = forest cover at kill site (1) or not (0).

this case we expected that maternal females should spend the least time feeding at kills when interspecific influences are greater than intraspecific influences. We also examined the hypotheses that male and female cougars might select for different species, sexes, and age classes of prey because of behavioral differences. Hence we explored whether, to maximize pursuit of mates and discourage incursions of breeding competitors, resident males killed larger and older prey (Murphy 1998; Mattson et al. 2007). We also investigated whether maternal females killed a greater proportion of small ungulate prey, which are easy to capture and potentially easier to train growing kittens to hunt than are larger prey (Murphy 1998; Anderson and Lindzey 2003; Mattson et al. 2007; Knopff et al. 2010b; K. R. White et al. 2011).

During the PW study, adult male cougars did exhibit lower affinity for their kills than did other cougars, presumably because their social motivation was heightened as the cougar population was establishing in the study area (Murphy 1998). Adult males spent a median 1 day less feeding at kills than did solitary or maternal females, yet they did not spend longer than females searching and hunting from one kill to the next [12]. In contrast, DW adult male cougars did not appear to minimize time at kills compared to females. Males spent a similar time handling kills as did solitary and maternal females—a median of 3 days. During wolf restoration, male cougars did spend longer searching and hunting

TABLE 6.6. Model averaged beta estimates and 95 percent confidence intervals from top linear regression models explaining variation in cougar kill rates during wolf restoration on the Greater Yellowstone Northern Range, 1998–2005.

| Term                                  | Beta (95% CI)       | Interpretation                                                                                                                                                                                                                           |
|---------------------------------------|---------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Displacement <sup>a</sup>             | 0.42 (0.15–0.68)    | Kill rate increased by 15% to 68% when displacement occurred                                                                                                                                                                             |
| 100 kg prey weight (PreyWt)           | 0.54 (0.35–0.69)    | Kill rate increased by 35% to 69% with a 100 kg increase in prey weight                                                                                                                                                                  |
| Adult male (Social) <sup>b</sup>      | −0.12 (−0.38–0.14)  | Data did not support a difference between adult males and adult females                                                                                                                                                                  |
| Maternal female (Social) <sup>c</sup> | −0.56 (−0.85–−0.27) | Maternal female kill rate was 56% lower than the kill rate of adult females, as kittens were included in the kill rate metric. However, maternal females were displaced more frequently from their kills than were other social classes. |
| Winter                                | 0.02 (−0.05–0.10)   | Data did not support a difference in kill rate between summer and winter                                                                                                                                                                 |

<sup>a</sup> Displacement by wolves and bears.

<sup>b</sup> Adult females are the reference category.

<sup>c</sup> Adult females are the reference category.

between kills than did maternal females, probably because maternal females were displaced from kills more frequently but also because maternal females moved less while feeding growing offspring [13]. Finally, PW adult males spent a median of 2 days less handling their kills than did their DW counterparts, but they did not differ in their search-hunting time between kills compared to their DW counterparts [14].

Although DW cougars overall killed a greater proportion of large prey, which might explain the longer handling and search-hunt times of DW adult males, cougar social classes killed similar-size prey within and between study phases [15]. This contrasted with findings in Washington state and across three study areas on the southern Colorado Plateau, where male cougars killed more elk (adult elk in the Washington study) and females killed more adult deer, deer fawns, and elk calves (Holton and Mattson 2011; K. R. White et al. 2011).

Because they, too, are traveling in search of mates, solitary females may also maximize time between kills when not supporting offspring while minimizing energy intake when handling kills. Prior to wolves, data supported this hypoth-



esis. Solitary females spent a similar amount of time at kills as did adult males and slightly less time than did maternal females [16]. Solitary females also spent a significantly longer time moving between kills—3 days longer than did PW males that were patrolling their territory and 2 to 4 days longer than PW maternal females [17]. Following wolf restoration, DW solitary females also maximized time between kills—spending 2 to 4 days longer before making the next kill than did DW maternal females [18]. Yet DW solitary females did not minimize time at kills; they instead spent 2 days longer handling kills (median = 4 days) than did maternal female cougars (median = 2 days) [19].

Comparisons between the two study periods further supported the hypothesis that PW solitary females minimized time at kills and maximized time traveling between kills. Solitary PW females spent roughly 2 days less feeding on kills and 3 days longer moving between kills than did solitary females during wolf presence [20]. As we followed solitary female cougars during kill rate sampling, we discovered that they moved beyond their typical boundaries used when rearing offspring. During these excursions, solitary females frequently scraped and spent time with males, sometimes different males, between feeding on kills. As young PW females were establishing territories and searching for new mates distributed at a low density across the study area, they were apparently maximizing time between kills to a greater degree than DW solitary females. An alternative explanation might be that females spent longer searching for and encountering prey prior to than during wolf restoration, but elk—particularly elk calves—were more abundant in the PW than the DW period.

In contrast to our predictions, maternal females did not appear to maximize food intake by minimizing time at kills when risk of predation from competitors was greater than intraspecific influences. Maternal females fed at kills for an average 2.5 days both prior to and during wolf restoration [21]. Yet DW maternal females did make another kill in less time—a median 1.5 to 2 days less—than did solitary females and adult males [22]. This presumably was because the energetic requirements of feeding growing offspring and displacements meant they had to kill again in a shorter amount of time than did solitary females and adult males. While killing the next prey item may be less risky than guarding the present one, the cost of obtaining a new meal may not always outweigh the risk associated with checking on

remaining food, particularly when provisioning offspring (Wilmers et al. 2003a). After cougars were forced from kills, we observed them return to check on carcasses even under risk of predation. This applied particularly to maternal females. In one instance, after being treed by wolves that did not feed on her kill, female F106 returned with her kittens and consumed the kill.

In combination, the data presented in this section suggest that it was easier for PW cougars to encounter prey and have time to consume what was needed to meet energy demands without concerns of frequent displacement. Adult males and solitary females potentially consumed large amounts in a short time, enabling them to spend a greater amount of time establishing social relationships and home range boundaries. Consequently, PW males did minimize time at kills and maximize time traveling between kills, either in search of mates or in territory defense, as male home ranges were larger and less stable and males overlapped with fewer females than during wolf restoration, which we cover in later chapters. In contrast, DW adult males may have spent longer at kills because of greater stability in male social structure and territories. Adult DW male and solitary female cougars maximized time consuming kills to a slightly greater degree than their PW counterparts, perhaps also reflecting fewer intraspecific and greater interspecific constraints. As cougars avoided wolves during wolf restoration, they were relegated to areas of lower elk use than the areas PW cougars used. Hence, although they did not roam to the extent of their PW counterparts, they still roamed in search of mates, and they searched for less abundant prey before making their next kill.

### Seasonal Influences

A seasonal effect was included in top models of both study phases, but the effect on kill rate was not clear when compared to other factors (tables 6.4 and 6.5). This uncertainty could be partly related to the fact that cougars killed adult elk in poor condition into May—defined as a summer month in our analyses—and thus seasonal comparisons were not clear-cut.

When we considered seasonal effects independent of our modeling and standardized kill rates by accounting for biomass of prey and biomass of cougars, PW cougars killed prey at a somewhat higher rate during winter than summer, but this was not the case during wolf restoration (fig. 6.6a, 6.6b; Murphy 1998) [23]. The difference in seasonal kill rates of

PW cougars and lack of seasonal difference for DW cougars was strongly influenced by the proportion of small ungulate prey relative to the proportion of large ungulate prey killed in each season. The proportion of small to large ungulate prey killed by PW cougars was much greater in summer relative to winter, while the proportions became much more equitable between seasons for DW cougars [24].

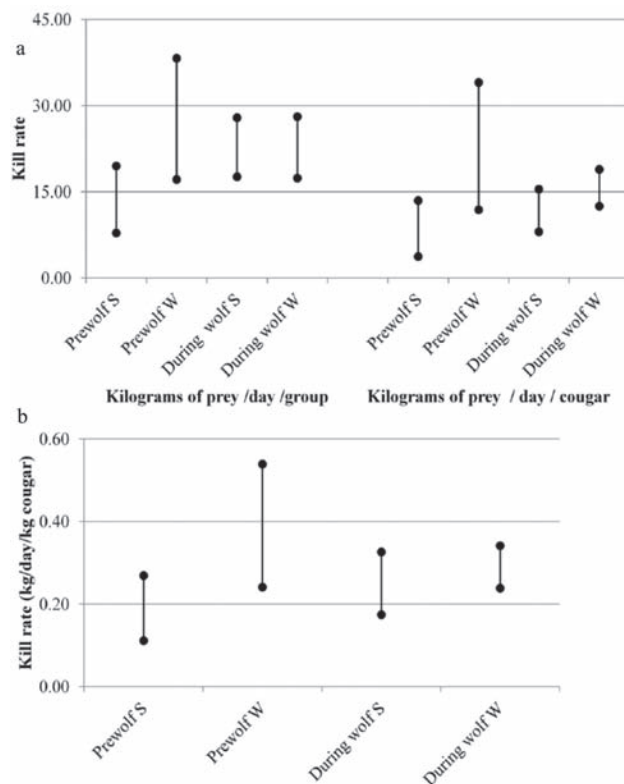
During wolf restoration, kill intervals of cougars did tend to shorten as the proportion of small ungulate prey, primarily elk calves, increased in the diet of DW cougars (fig. 6.7) [25]. This occurred primarily during June through December, when elk calves increased in availability, but coincided with an increased frequency of bears displacing cougars from their kills. When we removed displacements, the search-hunting time between kills was somewhat more strongly correlated with prey size, and handling time was less so [26].

### ENERGY EXPENDITURE OF COUGARS AND WOLVES

To understand the energy requirements of cougars and wolves and provide an initial picture of which carnivore should kill more frequently, we compared their *basal metabolic rate* (BMR) and *field metabolic rate* (FMR). The BMR, as a function of metabolic weight ( $70 \cdot \text{weight}^{0.75}$ ), reflects energy expenditure of an animal at rest in a thermally neutral environment—such as a sleeping cougar metabolizing only fat (Kleiber 1961). Under these circumstances the 4,706 kilojoule per day (kJ/day) BMR of a 40 kg female cougar is roughly the same BMR as for a 40 kg wolf. Because a cougar or wolf is rarely exclusively metabolizing fat in a resting state, FMR provides an improved estimate of total energy expenditure, including basal metabolism, thermoregulation, maintenance (such as lactation), and activity (Kreeger 2003). Once these essential energy requirements are met, extra energy can then be allocated to growth, fat deposition, and reproduction.

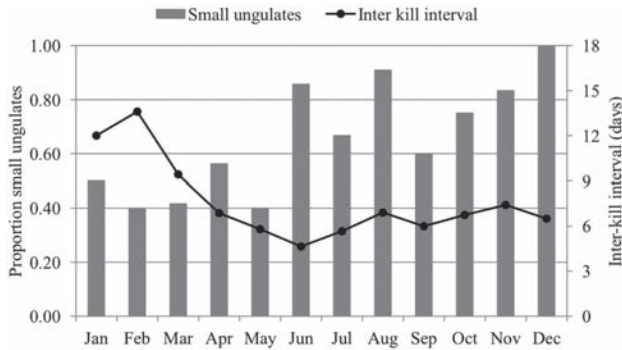
To enable comparisons to wolves, we calculated the FMR to BMR ratio for cougars using Laundré's (2005) estimates of daily energy expenditure for adult males and for females without kittens. We added energy costs for females with kittens at three months old and kittens supported through to the last month of dependence. We used values for wolves adjusted for weight and gender from Kreeger (2003) and Peterson and Ciucci (2003).

Although cougars and wolves can travel at high rates of speed, cougars are more prone to periods of rest than are



**FIGURE 6.6.** Cougars killed prey at a higher rate in winter ( $n = 24$ ) than summer ( $n = 15$ ) prior to wolves, while cougars during wolf presence killed prey at similar rates in winter ( $n = 50$ ) and in summer ( $n = 57$ ). Kill rates were quantified during kill rate sampling sequences and are presented as kilograms of prey per day per cougar group and kilograms of prey per day per individual cougar (a) and as kilograms of prey per day per kilogram of cougar (b).

wolves. Given differences in movements, adult male cougars and females without kittens use calories at about 2.3 times and 2.2 times BMR, respectively. When sustaining high rates of travel, wolves use calories at an estimated 4.6 to 5 times BMR (Kreeger 2003; Peterson and Ciucci 2003). Comparing this ratio as well as the FMR of similar weight cougars and wolves revealed that the rate at which wolves might use calories was at least twice the rate of solitary adult cougars. The FMR of a similar gender and weight wolf was 89 percent greater than that of a 53 kg adult male cougar (13,203.5 kJ/day) and 87 percent greater than that of a 40 kg solitary adult female cougar (10,164 kJ/day). The daily energy expenditure of a 40 kg female cougar supporting an average litter (2.6 to 2.9) of three-month-old kittens (19,235 kJ/day; Laundré 2005) was



**FIGURE 6.7.** Monthly proportion of small prey, primarily elk calves, in the diet of cougars and the average inter-kill interval each month during wolf restoration and colonization on the Greater Yellowstone Northern Range, Montana and Wyoming, 1998–2005.

similar to that of a solitary female wolf of similar weight (18,977 kJ/day). Once kittens reach their last month of dependence, their mother's estimated daily energy expenditure should increase substantially—to about 38,980 kJ/day (Laundré 2005). The combined energy expenditure of a female wolf and three pups equated to near 66,104 kJ/day, or 70 percent greater than the female cougar supporting dispersal-age yearlings (Kreeger 2003; Peterson and Ciucci 2003).

Because adult male and female cougars outweighed adult male and female wolves and energetic demand per unit mass declines as body mass increases, we used metabolic body mass (Peterson and Ciucci 2003) for comparisons among species. This adjustment revealed estimated energy requirements of 672 kJ/kg<sup>0.75</sup>/day for a 53 kg cougar and 1,270 kJ/kg<sup>0.75</sup>/day for a similar-size wolf. The female cougar supporting pre-dispersal offspring at a mean weight of 35 kg expended roughly 1,000 kJ/kg<sup>0.75</sup>/day compared to the female wolf and three 21 kg pups, which expended an estimated total of 1,990 kJ/kg<sup>0.75</sup>/day.

Per kilogram, a wolf expends at least double the energy of a cougar, suggesting that wolves should kill more frequently and consume more biomass than cougars. Limited information exists on the caloric content of different prey, with 7.7 kJ/g for prey carcasses one commonly used estimate (Glowacinski and Profus 1997). Given this estimate, wolves should need an average minimum daily energy requirement of about 3.25 kg of food/wolf/day, and solitary cougars should need an average of 1.4 kg/cougar/day (range = 1.4 to 5.1 kg/day for solitary versus maternal females) to meet their

minimum daily energy requirements. Wolves should also kill more frequently than cougars, as each kill must meet the energetic demands of a greater number and biomass of individuals within a pack. In the following sections we examine whether these predictions held and whether factors influencing kill rate differed for wolves from those for cougars.

## DID COUGARS AND WOLVES KILL AT SIMILAR RATES?

While we were busy completing predation sequences on cougars, the Yellowstone Wolf Project accomplished forty-two winter predation sequences on six wolf packs on the Greater Yellowstone Northern Range between 1998 and 2005 (Smith et al. 2004a). Radio-marked wolf packs were located from the ground and the air for thirty days in early winter (mid-November through mid-December) and late winter (March; Smith et al. 2004a). These winter predation sequences on wolves yielded a total of 482 ungulate kills—225 adult elk, 200 elk calves, 40 elk of unknown sex or age, 9 deer, 6 bison, and 2 moose. Summer kill rates of wolves were not available during our study phase but were later quantified by Metz and colleagues (2011), and we reference those rates in the following discussion. Kill rates of cougars during wolf restoration were similar between non-winter and winter; thus we used annual cougar kill rates for comparisons to winter wolf kill rates. While we used the ratio method for these comparisons, we did not find differences in estimates produced by the ratio and IKI methods for cougar kill rates [27].

We compared kill rates of cougars and wolves using four metrics:

1. Days/kill/predator group—calculated by dividing the number of days in the sampling period by the number of kills.
2. Kills/day/predator group—calculated by dividing the number of kills by the number of days in the sampling period in which the respective cougar, cougar family group, or wolf pack was detected.
3. Kg/day/predator—calculated by dividing the number of kills by the estimated cougar days or wolf days for a given cougar group (females with kittens) or pack for each period.
4. Kg/day/kg of predator—calculated by dividing the number of kills by the estimated cougar days or wolf days and by the total biomass for a given cougar, cougar group (females with kittens), or pack for each period.

**TABLE 6.7.** Mean annual kill rates (95 percent confidence intervals) of eleven adult and five subadult cougars and winter kill rates of wolves on the Greater Yellowstone Northern Range, 1998–2005. Kill rates were calculated with the ratio method (Hebblewhite et al. 2003; wolf kill data from Smith et al. 2004b).

| Kill Rate Estimate     | DW Cougars       |                  | Wolves               |                  |
|------------------------|------------------|------------------|----------------------|------------------|
|                        | Adults           | Subadults        | Adults and Subadults | All NR Packs     |
| Days/kill              | 8.2 (7.0–9.5)    | 13.6 (0.6–26.6)  | 9.3 (6.9–11.8)       | 3.2 (2.7–3.7)    |
| Kills/day              | 0.14 (0.12–0.16) | 0.11 (0.04–0.17) | 0.13 (0.11–0.15)     | 0.37 (0.32–0.41) |
| Kg/day/group           | 16.8 (13.5–20.1) | 12.7 (1.7–23.8)  | 16.1 (12.8–19.4)     | 79.5 (69.6–89.4) |
| Kg/day/carnivore       | 11.9 (8.8–14.9)  | 12.7 (1.7–23.8)  | 12.0 (9.0–15.1)      | 6.7 (5.9–7.5)    |
| Kg/day/kg of carnivore | 0.22 (0.18–0.27) | 0.30 (0.05–0.55) | 0.24 (0.18–0.29)     | 0.15 (0.13–0.17) |

### Comparison of Cougar and Wolf Kill Rates

Cougars killed ungulate prey less frequently than did wolf packs, annually averaging an ungulate kill every 9 days (0.13 kills/day/cougar or cougar family), but they fed on each kill for longer periods of time than did wolf packs (table 6.7; fig. 6.6) [28]. On average, wolf packs during winter killed and consumed an ungulate every 2 to 3 days (0.37 kills/day/pack; table 6.7; Smith and Bangs 2009). After we incorporated the size of prey into the kill rates, wolf packs killed almost five times the biomass that cougars killed—79.5 kg/day/pack compared to 16.1 kg/day/cougar—or twice the rate predicted from metabolic body mass predictions of energy expenditure [29]. These individual cougar to wolf pack comparisons highlighted our need to address total predation rates, which we cover in chapter 8, the summary chapter of this section.

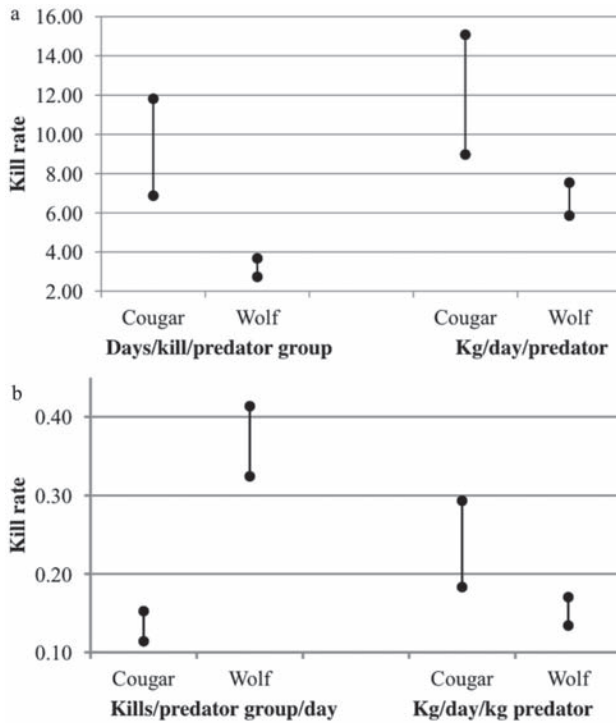
Wolf packs consisted of five to twenty-seven members feeding at each kill, whereas one to five cougars (females with kittens) fed at each prey carcass. After incorporating the numbers and biomass of predators at a kill (kg/day/predator and kg/day/kg of predator), we found that, per individual, cougars killed between 9.0 and 15.1 (95 percent confidence interval) kilograms per day, almost double the winter kill rate of wolves (fig. 6.8) [30]. We calculated wolf kill rates at 5.9 to 7.5 (95 percent confidence interval) kilograms per day for each wolf across the entire winter (table 6.7). These rates were similar to those reported by Stahler and colleagues (2006), who found that Greater Yellowstone Northern Range wolves may require 5.7 to 10.4 kg/wolf/day during early and late winter, respectively. Cougars also acquired prey at a higher rate when we included kilograms of each predator—an average rate of 0.24 kg/day/kg of cougar compared to the wolf rate of 0.15 kg/day/kg of wolf (table 6.7) [31].

In the years 2004 through 2009, after our study ended, Metz and co-workers (2011) estimated summer kill rates of wolves for packs. This work revealed that in summer, wolves acquired prey biomass at almost half the rate they did during winter. Average rates of daily prey acquisition decreased from 8.4 kg/wolf/day (SE = 0.9) in May to 4.1 kg/wolf/day (SE = 0.4) in July (Metz et al. 2011). The amount of biomass acquired per adult wolf also declined as pack size increased, but these rates were still above those predicted by caloric needs. In comparison, cougars acquired prey at a daily rate of 8.0 to 15.4 kg (95 percent confidence interval, not adjusted for edible biomass) per individual across all summer months—again, roughly twice that acquired by wolves.

Counting calories to determine the minimum daily energy requirements of wolves and cougars underestimated the rate at which wolves and cougars acquired prey. The productivity and survival of wolves have been found to decline when food availability falls below an estimated 3.25 kg/wolf/day (Mech 1977b; Peterson and Ciucci 2003). The total biomass acquired per wolf per day on the Northern Range was well above this minimum estimated intake and above the field estimates of 3.9 to 5.4 kg of elk/wolf/day reported by Becker and colleagues (2009b) for central Yellowstone wolves during winter. While a similar threshold has not been given for cougars, the total biomass acquired by cougars in our study also well exceeded the 1.5 to 4.8 kg/day/cougar or cougar family group estimated from energetic calculations and movement models in a deer-dominated system during summer in Idaho (Laundré 2005, 2008) [32].

Why might cougars acquire biomass of prey at double the rate of wolves when their energy requirements are predicted to be half those of wolves? In the Greater Yellowstone Ecosystem, scavengers and competitors may have strong





**FIGURE 6.8.** Comparison of cougar and wolf kill rates using four metrics of kill rate. Wolves kill at a higher frequency than cougars (days/kill/predator and kills/predator/day), but cougars acquire prey at a higher rate per biomass of prey (kg/day/predator) and per biomass of carnivore (kg/day/kg predator). This is in contrast to predictions based on energy requirements of each carnivore (see text). Kill rates were quantified during kill rate sampling sequences on cougars throughout the year and on wolves in winter.

influences on how much food is acquired and thus how frequently carnivores must kill. We address this discrepancy in the following section.

### What Influenced Kill Rates of Wolves?

While variation in the rates at which cougars killed prey was a result of the availability of large prey, displacements by dominant competitors, and maternal females killing at a higher rate than other adults, wolf kill rates were tied to winter severity and the number of wolves feeding at a kill (table 6.8). During more severe winters and as conditions harshened as winter progressed, wolves acquired prey at an increased rate (table 6.9). Elk became easier to pursue and capture because severe winters negatively affected their condition and because increased snow depths and colder

**TABLE 6.8.** Multiple linear regression models of variables explaining variation in kill rates (log of kg of prey/day/kg of carnivore) of cougars and wolves during wolf restoration on the Greater Yellowstone Northern Range, winters 1998–2005.

| Models <sup>a</sup>                   | AICc    | ΔAICc | K | w <sub>i</sub> | R <sup>2</sup> <sub>adj</sub> |
|---------------------------------------|---------|-------|---|----------------|-------------------------------|
| <b>COUGARS</b>                        |         |       |   |                |                               |
| Lnlarge + Disp + Social               | 39.33   | 0.00  | 7 | 0.19           | 0.63                          |
| Lnlarge + Disp + Social + Elev        | 40.52   | 1.20  | 8 | 0.10           | 0.63                          |
| Lnlarge + Disp + Social + Cougpop     | 40.75   | 1.43  | 8 | 0.09           | 0.63                          |
| Lnlarge + Disp + Social + Cougdensity | 40.84   | 1.51  | 8 | 0.09           | 0.63                          |
| Lnlarge + Disp + Social + Wolf        | 40.86   | 1.53  | 8 | 0.09           | 0.63                          |
| Lnlarge + Disp + Social + Temp        | 41.13   | 1.81  | 8 | 0.08           | 0.63                          |
| Lnlarge + Disp + Wolf                 | 42.02   | 2.70  | 6 | 0.05           | 0.62                          |
| <b>WOLVES</b>                         |         |       |   |                |                               |
| PackSize + WSI                        | -118.92 | 0.00  | 5 | 0.12           | 0.15                          |
| Packsize + Wolfpop + WSI              | -117.53 | 1.40  | 6 | 0.06           | 0.14                          |
| Packsize + Elev + WSI                 | -117.51 | 1.41  | 6 | 0.06           | 0.14                          |
| Packsize + Asinlarge + WSI            | -117.48 | 1.44  | 6 | 0.06           | 0.14                          |
| Packsize + Temp + WSI                 | -117.06 | 1.86  | 6 | 0.05           | 0.13                          |
| Packsize + Calf:cow Ratio + WSI       | -117.05 | 1.87  | 6 | 0.05           | 0.13                          |
| Packsize + Elkabundance + WSI         | -116.92 | 2.00  | 6 | 0.04           | 0.13                          |
| Packsize + Wolfuse + Elev + WSI       | -116.19 | 2.73  | 7 | 0.03           | 0.13                          |

<sup>a</sup> Winter was not included because earlier modeling and statistical tests indicated there was no difference in kill rate between summer and winter after wolf restoration.

temperatures inhibited their escape from wolves (figs. 6.9 and 6.10; Nelson and Mech 1986; Huggard 1993; Mech et al. 2001; Mech and Peterson 2003; White et al. 2009a, 2009b). In addition, as snow levels increased, wolves consumed a smaller percentage of their kills (Wilmers et al. 2003a)—presumably because the costs of acquiring the next prey item decreased with increasing snow depth.

The size and variability of wolf packs influenced how many members fed at a single kill, which in turn influenced the kill rates of each pack (table 6.9; Peterson et al. 1984; Jedrzejewski et al. 2002; Metz et al. 2011). During both summer and winter, gross food availability decreased with increasing numbers of wolves in a pack, and handling times dropped because more individuals devoured the kill in short order (Thurber and Peterson 1993; Schmidt and Mech 1997; Sand et al. 2005; Becker et al. 2009b; Metz et al. 2011). Including the biomass of wolves in our kill rate metric should provide an adjustment to reduce the effect of pack size. Instead, the kill rate

**TABLE 6.9.** Model averaged beta estimates and 95 percent confidence intervals from top linear regression models explaining variation in wolf kill rates during wolf restoration on the Greater Yellowstone Northern Range, 1998–2005.

| Term                                                                                                             | Beta (95% CI)             | Interpretation                                                              |
|------------------------------------------------------------------------------------------------------------------|---------------------------|-----------------------------------------------------------------------------|
| Pack size <sup>a</sup>                                                                                           | −0.003<br>(−0.005–0.0006) | Kill rate declined by <0.05% with increase of one individual in pack size.  |
| WSI <sup>b</sup>                                                                                                 | 0.024<br>(0.003–0.045)    | Kill rate increased by 1% to 5% with a 1 point increase in winter severity. |
| Wolf population, proportion large prey, temperature, calf:cow ratio, total elk count, and elevation <sup>c</sup> |                           | Data did not support a difference for these factors.                        |

<sup>a</sup> Wolf pack size ranged from 7 to 37.

<sup>b</sup> WSI = winter severity index ranging from −4 to 4.

<sup>c</sup> The 95% confidence intervals for wolf population size, proportion of large ungulate prey, temperature (°C), ratio of calves to cow elk, total elk abundance, and elevation spanned zero; thus the influence of these variables was not clear.

of wolves (kg of prey/day/kg of wolf) still declined as pack size increased. Kill rates may not change for several reasons. First, intake rates of wolves present at a kill may not decline, as the cohesiveness of a pack varies by season and initial pack size (Metz et al. 2011). Although pack attendance at kills during winter was greater than 90 percent at both large and small kills, overall, larger packs foraged less cohesively than smaller packs (Metz et al. 2011). Further, while smaller packs should kill less frequently and tend to have a higher biomass intake, the overall disparity between packs may not be so great given that kills of larger packs are less prone to scavenger loss than are kills of smaller packs (Becker et al. 2009b).

### PREY ACQUISITION: SOCIALITY, LOSS OF FOOD, AND PREY SIZE

The sociality of wolves and differences in their hunting and feeding behavior help explain discrepancies in kill rates between cougars and wolves that were in contrast to our predictions. For coursing predators like wolves, chasing and subduing prey is the main effort involved in killing (Creel and Creel 2002). The greater distances they chase prey, lower capture success rates of wolves, and social interactions within and between packs, in combination, result in greater energy demands than those of cougars (Husseman et al.

2003b; Mech and Peterson 2003; Peterson and Ciucci 2003; Miquelle et al. 2005). Per hunt, cougars appear more successful than wolves (Hornocker 1970) and take longer to consume prey, both of which equate to less energy expenditure than that of social and cursorial canids (see also Gorman et al. 1998; Miquelle et al. 2005). Why, then, do cougars acquire greater prey biomass than wolves and well beyond that predicted based on their energetic needs and hunting-feeding behaviors? We hypothesize that wolves may be more efficient consumers of carcasses, losing less to scavengers, competitors, and freezing in winter than do cougars, thus explaining the disparity between estimates based on energy expenditure and actual kill rates.

Scavenging and competitive interactions constrain food intake for wolves but perhaps even more so for cougars in the Greater Yellowstone Northern Range. Although both cougars and wolves dealt with at least twelve different scavengers, wolves potentially lost less biomass to scavengers because they initially consumed carcasses more quickly than did cougars (fig. 6.11; Stahler et al. 2002; Wilmers et al. 2003a, 2003b). Instead of concealing their kills, wolves must out-eat numerous scavengers and competitors, and they do so more effectively when pack numbers are greater (Murphy et al. 1999; Ballard et al. 2003). Although kill rates of large wolf packs were high, larger packs consumed a greater percentage of their prey, losing less to scavengers than did smaller or less cohesive packs (Wilmers et al. 2003a; Vucetich et al. 2004). The average Yellowstone pack of about eleven wolves immediately ate roughly 110 kilograms of a cow elk carcass weighing about 230 kilograms (Smith and Bangs 2009). In general, carcasses of prey killed by wolves rarely lasted more than forty-eight hours on the landscape (Stahler et al. 2006). Small wolf packs compete with scavengers to such an extent that they may have kill rates as high as larger packs to make up for losses to scavengers (Kaczensky et al. 2005; Smith and Bangs 2009). The greater proportion of large prey killed in late winter as our study progressed also likely equated to wolves gaining more biomass than cougars because they more quickly consumed carcasses and more readily defended them from scavengers. Thus, by forming large packs, individual wolves maximized their foraging returns, particularly when prey were large and vulnerability to scavenging losses was high (Vucetich et al. 2004).

Cougars may also be less efficient consumers than wolves when temperatures plunge, as carcasses become encapsu-



**FIGURE 6.9.** *Bison foraging in snow on the Greater Yellowstone Northern Range. Deep snow and winter severity not only influence the mobility of prey during an attack; they also decrease ungulate foraging efficiency and increase energy expenditure, ultimately resulting in weakened physiological condition over time. Photo by Toni Ruth, Hornocker Wildlife Institute/Wildlife Conservation Society.*

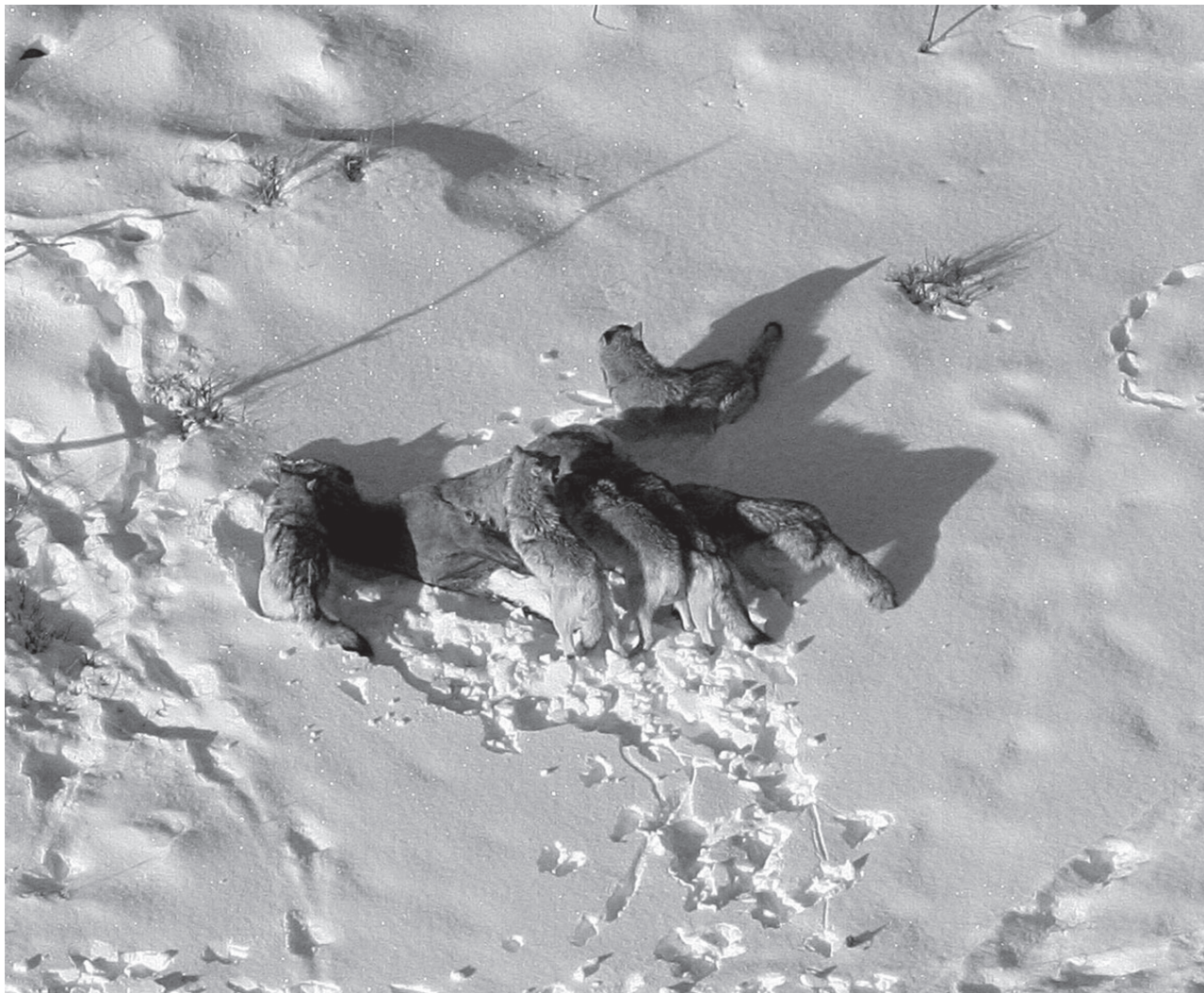
lated and frozen in wet snow. As cougars feed, an increasing surface area of meat is exposed, which then comes into contact with snow. Lacking feet and claws adapted to digging, cougars sometimes must abandon carcasses that become entombed in snow when temperatures drop well below freezing. Wolves plow into a carcass, snatching off chunks of meat and leg bones, eventually taking portions to nearby areas to feed. They readily crush and consume softer bone such as ribs. Cougars also consume some bone, but their carnassials are primarily adapted for sheering off chunks of soft tissue.

Whereas cougars and wolves are perhaps similarly efficient at consuming deer and elk calves, as cougars increasingly killed larger ungulate prey that were more difficult to conceal

from competitors, they potentially lost a greater amount of biomass to scavengers than did wolf packs. Longer handling times, particularly with large kills, resulted in increased odds of cougars being displaced from a kill, resulting in increased kill rates (also see chapter 7).

The variation around the estimates for displacements, proportion of large prey, and social class of cougars was quite large—probably because of true variability in cougar predatory behavior, such as whether a female was supporting young of the year or yearling kittens, and as related to the sporadic nature of displacements (table 6.10). Cougar family groups were more susceptible to displacements than were males or solitary females, and this appeared to be related primarily to





**FIGURE 6.10.** Elk, deer, and moose all become more vulnerable to wolf and cougar predation during harsh winters. Photo by Dan Stahler, National Park Service.

the frequency at which maternal females killed and secondarily to the size of prey. The most supported models for wolves explained between 0.13 and 0.15 of the variation in kill rate, leaving a substantial amount of kill rate variation unexplained. Likewise, our models for cougars prior to wolves explained between 0.13 and 0.19 of the variation. In contrast, our most supported models for cougars during wolf presence explained from 0.58 to 0.75 of the variation in kill rate. Perhaps including displacements or estimates of the amount of biomass lost to scavengers and bears in the wolf data might explain more of the variation in kill rate. These factors, including the greater cohe-

sion of wolf packs in winter and their greater ability to defend a carcass, may help explain why although energy expenditure suggests that per kilogram of predator, cougars should kill at a lower rate than wolves, instead cougars acquired biomass at about 1.7 times the rate of wolves.

### COMPARISONS OF KILL RATES WITH OTHER STUDIES

Aided by advances in technology, quantifying kill rates of cougars, wolves, and other felids (e.g., jaguars, African lions, lynx) has blossomed since the early 2000s in a hand-



ful of locations (e.g., Anderson and Lindzey 2003; Sand et al. 2005; Webb et al. 2008; Cavalcanti and Gese 2010; Knopff et al. 2010b; Tambling et al. 2010; Krofel et al. 2012). Across study systems the frequency with which cougars killed prey ranged from 2.9 to 11 days per ungulate per individual cougar or family group, yet making comparisons among various systems remains challenging (Murphy 1998; Knopff et al. 2010b). Lower kill rates associated with the elk-dominated Greater Yellowstone Northern Range appear related to the fact that when not displaced from their kills, cougars spend more time consuming elk than mule deer, enabling them to invest more time in other behaviors before killing again (Murphy 1998; Murphy and Ruth 2010) [33]. Cougars in deer-dominated systems should kill more frequently to sustain themselves and their growing offspring (see Murphy and Ruth 2010; Knopff et al. 2010b). Cougars should also be more efficient at consuming small kills because they can do so more quickly, thus reducing losses to scavengers and competitors. Jaguars in the Pantanal, Brazil, with a diet consisting of 64 percent prey we considered small, including caiman (*Caiman crocodiles yacare*) and peccary (*Tayassu pecari* and *Pecari tajacu*), killed prey at a decreased frequency as prey size increased because they spent longer feeding on kills and a greater amount of time before making the next kill (Cavalcanti and Gese 2010). While an increased frequency

of killing prey during summer might be expected for carnivores that occupy systems where ungulates exhibit a synchronized birth pulse, as proposed by Knopff and colleagues (2010b), the effects of winter should not be overlooked in all systems. In systems where deer predominate, summer kill rates of cougars might be consistently higher than winter rates because fawns are abundant, and all deer age-sex classes are more equally vulnerable to cougars compared to age-sex classes of larger ungulate prey (Murphy 1998; Knopff et al. 2010b). In Yellowstone, where elk predominated, encounter rates with vulnerable individuals enhanced kill rates of pre-wolf cougars and of cougars in winter during wolf restoration. In early winter, when prey were in relatively good condition and harder for wolves to subdue, the rate at which wolves killed prey was generally less than in late winter (Smith 2005; Smith and Bangs 2009).

Carnivore kill rates not only influence prey but are also influenced by changes in the availability and vulnerability of prey. As we have outlined, as the proportion of small to large prey changed over time, so did cougar kill rates and displacement of cougars from kills. Consistency in defining prey as large or small and providing the proportion of large to small prey available across months or years will permit further comparisons of predation in various systems. For example, our use of >90 kilograms to classify prey as large contrasts



**FIGURE 6.11.** After emerging from hibernation in March and April, grizzly bears raid both cougar and wolf kills. Photo by Dan Stahler, National Park Service.

**TABLE 6.10.** Model averaged beta estimates and 95 percent confidence intervals from top linear regression models explaining variation in cougar kill rates during wolf restoration on the Greater Yellowstone Northern Range, 1998–2005.

| Term                                  | Beta (95% CI)      | Interpretation                                                                     |
|---------------------------------------|--------------------|------------------------------------------------------------------------------------|
| Displacement <sup>a</sup>             | 0.61 (0.22–0.99)   | Kill rate increased by 22% to 99% when displacement occurred.                      |
| Proportion large prey (Large)         | 0.29 (0.081–0.49)  | Kill rate increased by 8% to 49% with a 1% increase in proportion of large prey.   |
| Adult male (Social) <sup>b</sup>      | 0.10 (–0.35–0.56)  | Data did not support a difference between adult males and adult females.           |
| Maternal female (Social) <sup>c</sup> | –0.48 (–0.95–0.02) | Maternal female kill rate was 2% to 95% lower than the kill rate of adult females. |

The 95 percent confidence intervals for the variables of elevation, cougar population, cougar density, wolf use, and temperature spanned zero; hence the influence of these variables was not clear.

<sup>a</sup> Displacement by wolves and bears.

<sup>b</sup> Adult females are the reference category.

<sup>c</sup> Adult females are the reference category.

with the decision of Cavalcanti and Gese (2010), who classified large prey as those  $\geq 30$  kilograms. A simple ratio using female cougar biomass to prey biomass is roughly 1:2 for elk calves and 1:5.5 for adult elk [34]. By comparison, this ratio for mule deer, pronghorn, and bighorn sheep is 1:1. Even a ratio of relative risk may be simplistic in that it does not include seasonal changes in vulnerability of prey or the fact that some prey may pose higher risk relative to their small size (e.g., alligators in Florida, antlered male deer), but it may provide an initial step to compare data between systems.

Estimates based on inter-kill interval may also perform poorly as the metric for comparing across study areas. Including the biomass of prey and biomass of carnivores to standardize kill rates in our system supported Murphy's (1998) findings that PW cougars killed at lower rates during summer than winter and revealed that cougars were killing prey at twice the rate of wolves. Standardizing kill rates by including biomass of prey and predator may limit confusion when comparing across years, seasons, species, and systems. For instance, in a deer-dominated system in Alberta, Canada, cougars killed at one of the highest reported frequencies (days per kill), but this translated to 2.88 to 18.6 kg/day/individual—a range that was very similar to that of Northern Range cougars. Patagonian pumas also killed ungulate prey at a sim-

ilar rate of 6.7 to 18.3 kg/day/cougar (Elbroch and Wittmer 2013). Pumas in this system spent longer consuming kills of greater weight and those they could conceal well, while their handling time of prey decreased in the presence of condors.

In addition to standardizing kill rates, assessing factors that influence prey selection and kill rates at various times, between species, and between various study systems is furthering knowledge of carnivore predation more than simply comparing how frequently they kill. In systems devoid of large competitors, intraspecific social influences appear to play a stronger role in influencing kill rates, with the stability of home ranges and social interactions influencing energy-maximizing and time-minimizing strategies, particularly for adult male and solitary female cougars. As in our PW study, adult male cougars in Arizona maximized their intake of energy in the minimum time possible, thus enabling an opportunity to maximize time traveling and monitoring much larger areas than would otherwise be the case (Mattson et al. 2007). More work in this area is needed to address whether greater stability of cougar populations reduces kill rates to levels substantially below those of populations with high turnover (i.e., those heavily hunted). In systems containing multiple large competitors, interspecific social influences may alter the energy-maximizing and time-minimizing strategies of the various social classes. Greater Yellowstone Northern Range cougars, now clearly experiencing a landscape of fear harboring increased risks, are operating under a different set of tradeoffs that affect their kill rates compared to their PW counterparts.

## SUMMARY

The frequency at which cougars killed prey did not increase substantially following the restoration of wolves, but energy-maximizing and time-minimizing strategies as related to differing intraspecific and interspecific constraints affected handling time and movement between kills in dissimilar ways. Prior to wolf restoration, adult males and solitary females maximized energy intake at kills, males doing so within a day or two, and they maximized time moving between kills. As food was readily available, kill rates reflected their need to acquire energy balanced with expending energy to establish and defend territories and search for mates. The rate at which cougars acquired prey during wolf restoration reflected the combined influence of killing large prey and frequently losing carcasses to competitors.

Compared to cougars, wolves killed prey with greater frequency consistent with their coursing hunting and social behaviors and their feeding as a large cohesive group in winter. In contrast to predictions from energetic models, both cougars and wolves killed prey at higher rates than expected, and cougars killed at almost twice the rate of wolves when the biomass of prey and predator was considered. Because larger groups more easily defended and more quickly consumed large prey, wolves appeared to be more efficient consumers of kills, with less overall waste than cougars. Feeding on kills for at times close to a week led to greater chances of interference competition on large kills and of meat loss as a result of freezing when temperatures plummeted. Although the frequency at which cougars and wolves acquired prey is important within a system, comparisons of kill rates among species, time periods, and study areas is perhaps best accomplished by standardizing kill rates and, more important, understanding the energy-maximizing and time- and risk-minimizing intra- and interspecific factors that influence handling time of prey, as well as search-hunting time spent prior to making the next kill.

### **Text Box 6.1. The Small Stuff**

In early summer 2001 we did not document a single ungulate kill during our 41-day kill rate sampling on subadult female F112. She instead apparently subsisted primarily on blue grouse and marmots. She also killed but did not consume a red fox.

As we followed the eighteen-month-old subadult M126 during a predation sequence during winter 1999, he occupied a small area within adult male M137's home range (see fig. 17.1). During the 36 days we monitored M126, his movements were restricted to an area of roughly 4.7 km<sup>2</sup>. Although he was unsuccessful at subduing one elk, he successfully killed four elk during the monitoring sequence. He spent 7 days at kill number three and made kill number four the very next day, where he spent 8 days, lingering at both these kills well beyond the time it would have taken to consume them based on their size. Knopff and colleagues (2010a) also report some cougars killing ungulate prey at intervals greater than 21 days, the longest of which lasted 75 days, and surviving these intervals by consuming small mammals, birds, or carrion; but they do not specify if these were primarily subadult cougars.

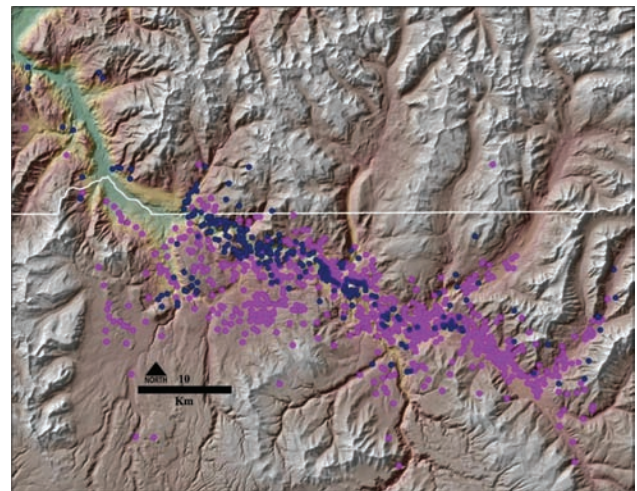
## CHAPTER 7

### Direct Interactions at Kills

Carcasses of prey are a patchy yet rich ephemeral resource across the Greater Yellowstone landscape (Keddy 2001; DeVault et al. 2003; Wilmers et al. 2003b). Each carcass is generally present as usable meat and tissue for only hours to days and then disappears from the landscape (Murphy 1998; Wilmers et al. 2003b). Bones are the exception—they contain calcium, phosphorus, sodium, magnesium, and protein, which rodents such as squirrels and porcupines utilize over a longer time frame (Havera 1978; Roze 1989; Robbins 1993). Severe winters, droughts, old age, disease, large predators, and humans create carcass patches, but a diverse group of secondary consumers exploits them (Wilmers et al. 2003b; Bischoff-Mattson and Mattson 2009; Smith and Bangs 2009). The variety of species drawn to these food patches might encounter one another and interact. Although direct interactions can occur, the profit of obtaining such nutrition might outweigh the associated risks of injury or death, and sometimes they are symbiotic interactions that are *mutualistic* or *commensal* (Lima and Dill 1990; Houston et al. 1993; Begon et al. 1996). In particular, ravens adopt a foraging strategy of following wolves to locate their kills—routinely gaining 2 to 20 kilograms of food per day from carcasses of wolf-killed prey (Stahler et al. 2002; Vucetich et al. 2004). Reproduction in bald eagles, magpies, and ravens is also tied to the availability of winter carrion (Swenson et al. 1986; Dhindsa and Boag 1990; Wilmers et al. 2003a).

Out of a carnivore's daily habits of resting, searching for mates, patrolling home range boundaries for intruders, and raising offspring, feeding at a kill is likely to draw the most attention from scavengers and competitors in ecosystems with multiple carnivores. As an example of the distribution of carcasses between 1998 and 2005, figure 7.1 shows the locations of cougar- and wolf-killed prey on Yellowstone's

Northern Range. The cougar's solitary nature may predispose it to adverse effects of displacement where frequent loss of meals might be energetically costly, and then direct interactions might lead to the cougar's injury or death (Boyd and Neale 1992; Murphy et al. 1998; Ruth 2004a). Yet certain characteristics of the landscape might enable cougars to avoid encounters with competitors and enhance their survival in a risky landscape. What characteristics of cougar-killed prey and the landscape might explain displacement of cougars from their kills by wolves and bears? Alternatively, what landscape and prey characteristics enable cougars to conceal and retain kills from competitors more successfully? We addressed these questions by assessing characteristics that best explained variation in the detection of cougar kills



**FIGURE 7.1.** Distribution of cougar kills (dark blue) and wolf kills (purple) within and adjacent to Yellowstone National Park's northern boundary (white line), 1998–2005.



**TABLE 7.1.** Predictions resulting from the hypothesis that variation in detection of cougar kills by dominant competitors is influenced by size of cougar-killed prey, competitor use of the landscape (wolves), availability of other foods (bears), characteristics of the landscape, and season associated with reproductive and feeding behaviors of competitors.

| <i>Independent Variable</i>                                                        | <i>Rationale and Predictions</i>                                                                                                                                                                                                                                                                                                                                                                                                    | <i>References</i>                                                                  |
|------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------|
| Wolf                                                                               | Wolves dominate cougars at and displace them from their kills.<br>P1: Wolf displacement of cougars from their kills increases as the use/density of wolves increases.<br>No similar variable for bear use was available.                                                                                                                                                                                                            | Ruth 2004a; Kortello et al. 2007                                                   |
| Prey size (yearling and adult elk = large prey, all other ungulates = small prey)  | Cougars feed longer on and have greater difficulty concealing large ungulate prey. Grizzly bear use of carcasses in spring increases with a greater amount of edible biomass.<br>P1: The odds that a cougar will be displaced by wolves or bears are expected to increase for large prey compared to small ungulate prey.                                                                                                           | Green et al. 1997; Murphy et al. 1998                                              |
| Wolf season (late fall/winter = Oct through Mar, spring/summer = Apr through Sept) | Overlap of cougars, wolves, and prey is greatest during winter and cougars kill a greater proportion of large prey, for which vulnerability increases as winter progresses. Wolf activity is localized around a den in spring and rendezvous sites during summer.<br>P1: Wolves are more likely to encounter and displace cougars from cougar kills during winter compared to non-winter months.                                    | Ruth 2004a; Alexander et al. 2006; Kortello et al. 2007                            |
| Bear season (spring/summer = Apr 1 through Jul 31, fall = Aug 1 through Nov 30)    | After emerging from dens and prior to green-up of vegetation in spring and early summer, ungulate carcasses are an important food for bears.<br>P1: Bears locate and displace cougars from kills more frequently in spring/summer than during the fall when foods are more abundant.                                                                                                                                                | Mattson 1997; Green et al. 1997; Murphy et al. 1998                                |
| Spring carcass count                                                               | Carcasses of ungulates are an important spring food for bears post-emergence from winter dens.<br>P1: As the number of available carcasses increases, the odds of a cougar being displaced by bears decline.                                                                                                                                                                                                                        | Mattson 1997; Green et al. 1997; Murphy et al. 1998                                |
| Whitebark pine (cone counts)                                                       | Seeds from whitebark pine are one of the most important autumn foods of bears in the Greater Yellowstone Ecosystem, and bears focus less on carcasses in years of high cone production.<br>P1: If bears also focus less on kills of cougars in autumn during years with good whitebark pine cone production, we predicted that odds of bears displacing cougars would be lower.                                                     | Mattson 1991, 1992                                                                 |
| Food                                                                               | A combination of availability of other foods during the year, as indexed by whitebark pine and spring carcass availability combined, reduces the likelihood that bears search for and encounter cougar kills.<br>P1: The odds that bears displaced cougars from their kills decreased with increasing availability of other foods.                                                                                                  | Mattson 1991, 1992                                                                 |
| Slope (degree at cache site)                                                       | Wolves traverse, hunt, and travel through habitats at lower slopes.<br>P1: The odds that a cougar will be displaced by wolves are greater for cougar kills occurring on lower slopes.                                                                                                                                                                                                                                               | Ruth 2004a                                                                         |
| Elevation (meters)                                                                 | Carcasses accumulate at low elevations in winter. Grizzly bear use of carcasses increases with increasing elevation in spring, and black bear use of carcasses declines with increasing elevation in late spring and summer.<br>P1: The odds that cougars are displaced from kills by wolves decrease with increasing elevation.<br>P2: The odds that cougars are displaced from kills by bears increase with increasing elevation. | Green et al. 1997; Murphy et al. 1998                                              |
| Forest cover and topographic roughness index                                       | Forest cover and topographically complex terrain enhance concealment of cougar kills. Interference competition occurs more frequently in open grasslands.<br>P1: The odds that wolves and bears displace cougars from their kills should be lower in forested and topographically complex terrain compared to open habitats.                                                                                                        | Beier et al. 1995; Creel and Creel 2002; Mattson et al. 2007; Murphy and Ruth 2010 |

by dominant competitors with a set of predictions about each of the variables we expected would have an influence—size of the prey killed, competitor use of the landscape (wolves), availability of other foods (bears), characteristics of the landscape, and temporal variation associated with reproductive and feeding behaviors of competitors. We present our research hypotheses and predictions in chapter 4 and table 7.1 and later discuss consequences of interference competition on cougar predation rates and energetic demands, how cougar kills benefit other species, and behaviors relevant to interaction at kills.

## DOCUMENTING VISITS AND DISPLACEMENTS

In our analyses we used the following definitions. *Detections* were any *visit* by another carnivore to a cougar kill and included *scavenging*, *displacements*, or unknown activity. Avian and mammalian species that fed from cougar kills but were unable to displace cougars from kills were considered to be *scavenging* at kills. These subordinate species presumably fed while cougars were bedded near a kill and after cougars had departed from the kill site. We considered *scavenging* also to have occurred when a dominant carnivore arrived at a kill after the cougar consumed the kill and departed from the kill site. A *displacement* occurred when a dominant species forced a cougar from its kill prior to the cougar completing consumption of the kill.

Detections of cougar kills by other carnivores were documented during predation sequences, opportunistically during winter track surveys and weekly aerial telemetry flights, and by searching clusters of cougar locations downloaded from GPS collars. The rugged topography and tree cover interspersed with more open habitats on the Greater Yellowstone Northern Range substantially assisted our location efforts. We were often able to observe cougars from a distance while locating them because, for example, we were hidden on a ridge above and distant from where the cougar was situated. When cougars were moving while we tried to locate them, we stayed distant until they stopped—sometimes following them for six to eight hours before they did so. With our techniques, during our daily forays to locate the focal cat we obtained observations of bears and wolves approaching or already at thirty-eight cougar kills. When we did not directly observe competitors and scavengers at kills, we determined their presence from tracks, hair, scats, feath-

ers, whitewash on trees and rocks from avian scavengers, and feeding behavior at the carcass. We categorized kills using accumulated evidence from radio-collar locations, observations, and hair, track, scat, and other signs at the kill site to determine the predator responsible for kills and scavengers present (appendix A). We also used remotely downloaded GPS locations of cougars and wolves, overlaid the locations in a Geographic Information System (GIS) environment, and considered a cougar kill to have been detected if overlay locations were within 375 meters (the upper bound of the 95 percent confidence interval for aerial telemetry error) and within less than five days.

*Displacement* of a cougar from its kill by another carnivore required direct observation of the carnivore taking over the kill or evidence that another carnivore visited a cougar kill in less time than a cougar normally required to consume a kill of that prey size. We were conservative in designating displacements when they were not directly observed and used the upper 95 percent confidence interval of the average number of days required for a DW cougar to finish a kill of a given size—five days for large ungulate prey and three days for small ungulate prey. Visits by wolves or bears after that time frame were considered potential *scavenging* events. There were times when we could not confidently distinguish between displacement and scavenging. Therefore positive displacements were retained, and all other visitations, including scavenging and scavenging with potential displacement, were removed from analyses of factors that influenced displacement and whether kill rates of cougars increased as a result. Further, 12 percent of field examinations occurred more than twenty-one days after a cougar made a kill, and evidence of wolf or bear visitation at the carcass was no longer discernible. Hence, for analyses of displacements, we limited data to kills we investigated within fourteen days or less from the date of death.

Although our data were not sufficient to assess how frequently cougars and wolves interacted away from kills, Wolf Project biologists observed wolf packs almost daily, particularly during winter predation studies conducted in November to December and March of each year (Smith et al. 2005). These intense field periods yielded direct observations of cougar and wolf interactions on at least five occasions.

## WHICH SPECIES DETECTED COUGAR KILLS?

During wolf restoration, 62 percent of cougar-killed prey ( $n = 468$ ) were detected by six avian and six terrestrial spe-

cies. We documented visits to 291 cougar kills by ravens (*Corvus corax*, 67%), magpies (*Pica pica*, 47%), coyotes (42%), grizzly and black bears (30%), golden eagles (16%), wolves (13%), bald eagles (*Haliaeetus leucocephalus*, 8%), foxes (2%), and other cougars (2%); and at two different cougar-killed ungulate carcasses we observed a gray jay (*Perisoreus canadensis*) and a northern goshawk (*Accipiter gentilis*) scavenging. Table 7.2 provides numbers for eight of these scavengers. Diversity of scavenger species was similar at wolf kills, with the list of species differing only slightly—four carnivores and eight avian species scavenged at wolf kills (Wilmers et al. 2003a, 2003b; Smith 2005; Smith and Bangs 2009). During our kill rate sampling sequences, 70 percent of the time we recorded at least one scavenger species present at the site of a cougar-killed ungulate carcass on the presumed date of death.

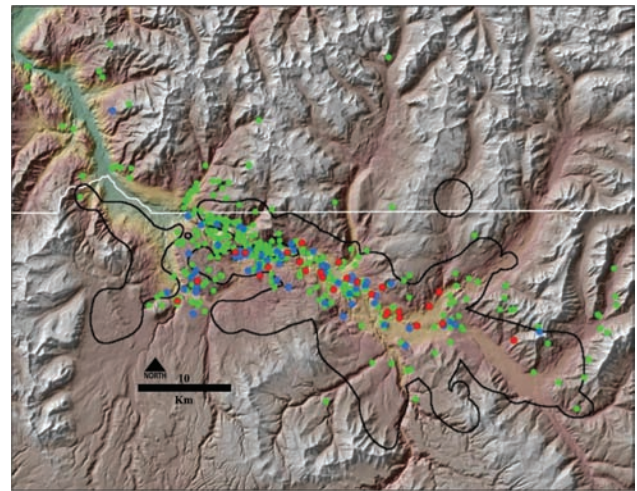
Despite cougars' attempts to conceal carcasses through caching or hiding carcasses under cover, scavengers—particularly ravens and magpies—were capable of discovering fresh cougar kills very quickly. Of kills scavengers visited, 57 percent were cached under trees or shrubs compared to 31 percent that were cached in open vegetation and 12 percent where we were unsure if the kill was hidden under trees or shrubs at some point. Unlike studies documenting food gains to ravens, condors (*Vultur gryphus*), and other carnivores through direct observation, we were unable to determine the degree of utilization by scavengers upon discovery of fresh carcasses (Wilmers et al. 2003a; Vucetich et al. 2004; Kaczensky et al. 2005; Elbroch and Wittmer 2013).

## DISPLACEMENT OF COUGARS FROM KILLS

Although at least twelve species visited cougar kills in Yellowstone, wolves and bears appeared to be the only two species effective at displacing the cats from kills. Prior to wolf restoration, both black and grizzly bears visited about 33 percent of cougar kills—bears scavenged about 1 in 3 kills and displaced cougars from about 1 in 8 kills (table 7.3; Murphy et al. 1998). During wolf restoration there were 358 cougar-killed ungulates that we investigated in the field within fourteen days. Of these cougar kills, wolves visited about 1 in 4 and displaced the cougar from 1 in 13 kills (fig. 7.2). When bears were active outside dens, they visited kills at which they displaced cougars at over twice the rate of wolves [1]. After we limited bear detection data to 190 cougar kills site-searched within fourteen days, bears visited about

**TABLE 7.2.** Proportion of visits and average number of individuals per visit of eight mammalian and avian scavengers documented at 291 of 468 cougar kills on the Greater Yellowstone Northern Range, 1998–2005.

| Species      | Proportion Visits | Average # Individuals/Visit | SD   | Range |
|--------------|-------------------|-----------------------------|------|-------|
| Wolf         | 0.13              | 4.39                        | 5.31 | 0–27  |
| Coyote       | 0.42              | 1.50                        | 0.92 | 0–5   |
| Fox          | 0.02              | 1.00                        | ...  | 0–1   |
| Bears        | 0.30              | 1.07                        | 0.30 | 0–3   |
| Magpie       | 0.47              | 3.70                        | 3.41 | 0–18  |
| Raven        | 0.67              | 4.60                        | 6.39 | 0–45  |
| Golden eagle | 0.16              | 1.26                        | 0.53 | 0–3   |
| Bald eagle   | 0.08              | 1.82                        | 0.85 | 0–4   |



**FIGURE 7.2.** Distribution of cougar kills that were detected by wolves (blue dots), from which cougars were displaced by wolves (red dots), or that remained undetected (green dots) on the Greater Yellowstone Northern Range, 1998–2005. The black line encloses the cumulative winter core area of all wolf packs, and the white line is the northern boundary of Yellowstone National Park.

1 in 2 cougar kills (95 of 190, or 50%) in non-winter months. They displaced the cougar from roughly 1 in 5 of these kills, although we could not always discern the species of bear that used cougar-killed prey. During wolf restoration, 21 of the 190 kills (11 percent) were detected by both bears and wolves (table 7.3). Wolves displaced cougars more frequently during winter, and bears displaced cougars during non-winter months [2]. In combination, total displacements by wolves and bears were greatest during non-winter months.

**TABLE 7.3.** Frequency at which bears and wolves detected cougar-killed ungulates and displaced cougars from kills on the Greater Yellowstone Northern Range, Montana and Wyoming, 1992–2005.

| Competitor         | Pre-Wolf (1992–95)    |            |               | During Wolf (1998–2005) |            |               |
|--------------------|-----------------------|------------|---------------|-------------------------|------------|---------------|
|                    | Total Kills in Sample | Detections | Displacements | Total Kills in Sample   | Detections | Displacements |
| Bears              | 58                    | 19 (33%)   | 7 (12%)       | 190                     | 95 (50%)   | 42 (22%)      |
| Wolves             | n/a                   | n/a        | n/a           | 358                     | 82 (23%)   | 27 (7.5%)     |
| Total <sup>a</sup> |                       |            |               | 358                     | 156 (44%)  | 67 (19%)      |

<sup>a</sup> Both wolves and bears detected twenty-one of the same kills, and both carnivores displaced cougars from two of those kills.

## FACTORS CONTRIBUTING TO DISPLACEMENTS BY COMPETITORS

As with cougars, life history traits and behaviors of wolves and bears were not constant during the year, and their behavioral changes presumably influenced detection and displacement of cougars from their kills. Based on wolf denning and pup-rearing patterns, we included two seasons in our assessment of factors that may influence wolf displacement of cougars from kills (late fall/winter: November 1–March 30, and spring/summer: April 1–October 31; table 7.1). Late fall/winter encompassed the period when wolf packs remained cohesive in their travel and hunting movements. During late winter and early spring, their movements became more centralized around the den (Metz et al. 2011). As pups matured in spring, individual wolves traveled greater distances during hunting forays away from rendezvous areas where most wolf movement was centralized (D. Smith, National Park Service, pers. comm., September 2003). In summer ungulate prey became more widely distributed and smaller mammals, such as leporids and rodents, became available as prey, which we expected to relax foraging on dead prey by wolves (Murphy 1998; Murphy and Ruth 2010). Because wolf use of the landscape was highly variable, which might influence detection of carcasses to scavenge, we developed a wolf use variable as a relative measure of how often wolves used particular areas. As such, “wolf use” approximated intensity of wolf use in the vicinity of a cougar kill during the year and season in which a cougar kill took place (appendix E).

Bear behaviors presented a different scenario from wolves: bears hibernated in dens during winter. We recorded no bear detections of cougar kills during December 1 through March 31, and we excluded winter kills from our analysis. Bears focused on different foods as they became available through the spring, summer, and fall (Mattson et al. 1991; Schwartz et al. 2006a). Prior to the appearance of vegetative forage

with the spring growing season, there were limited foraging opportunities for bears, and bears sought out carcasses for scavenging (Green et al. 1997; Mattson 1997). As availability of vegetation and insects increased during summer, bears took advantage of these other foods—particularly ants (Formicidae), horsetails (*Equisetum arvense*), graminoids, and forbs (*Cirsium scariosum*; Mattson et al. 1991). Berries, whitebark pine nuts, ungulates, rodents, and carrion provided important fall foods for bears (Kendall 1983; Mattson et al. 1991, 1992). Given these seasonal dietary changes, we defined seasons based on bear den emergence and entry dates and the availability of bear foods (spring/summer: April 1–July 31, and fall: August 1–November 30; Schwartz et al. 2006b). Because other important foods besides cougar-killed prey were available to bears, we included two variables for which data existed: (1) yearly Northern Range spring carcass counts and (2) yearly average fall whitebark pine cone counts for the Greater Yellowstone Ecosystem (Haroldson and Podruzny 2004, 2005, 2006; Podruzny and Gunther 2004, 2005; Schwartz et al. 2006b).

To find out which characteristics best explained variation in wolf and bear displacement of cougars from their kills, we used logistic regression and Akaike’s information criterion (with sample-size correction, AICc) to evaluate a set of a priori models (Akaike 1983; Burnham and Anderson 2002). Displacement of cougars from their kills by wolves was strongly influenced by size of the prey carcass, wolf use, and slope (model 1, table 7.4) [3]. Prey size, season, carcass count, and slope (models 1 and 2, table 7.5) all strongly affected the odds that a bear would displace a cougar from its kill [4].

## Prey Size

The risks associated with killing adult elk and other large-bodied prey extend beyond those associated with pursuit and capture in steep, rocky, or wooded terrain, in which



**TABLE 7.4.** Influence of prey and landscape characteristics on the odds of wolves displacing a cougar from a kill on the Greater Yellowstone Northern Range, 1998–2005. Information-theoretic results for candidate logistic regression models used to assess a kill sample of 303 cougar-killed ungulates.

| <i>Model<sup>a</sup></i>                       | <i>AICc</i> | $\Delta AICc^b$ | <i>Parameters<sup>c</sup></i> | <i>w<sub>i</sub><sup>d</sup></i> | <i>ROC AUC<sup>e</sup></i> |
|------------------------------------------------|-------------|-----------------|-------------------------------|----------------------------------|----------------------------|
| Wolf + Slope + Preysz                          | 154.0       | 0.0             | 5                             | 0.25                             | 0.82                       |
| Wolf + Slope + Preysz + Elev                   | 155.6       | 1.6             | 6                             | 0.11                             | 0.82                       |
| Wolf + Slope                                   | 156.0       | 2.0             | 4                             | 0.09                             | 0.81                       |
| Wolf + Slope + Preysz + Season                 | 156.0       | 2.0             | 6                             | 0.09                             | 0.82                       |
| Wolf + Slope + Preysz + Forest                 | 156.0       | 2.0             | 6                             | 0.09                             | 0.82                       |
| Wolf + Slope + Preysz + TRI                    | 156.1       | 2.0             | 6                             | 0.09                             | 0.80                       |
| Wolf + Slope + Preysz + Elev + TRI             | 157.6       | 3.6             | 7                             | 0.04                             | 0.81                       |
| Wolf + Slope + Elev                            | 157.6       | 3.6             | 5                             | 0.04                             | 0.81                       |
| Wolf + Slope + Season                          | 158.0       | 4.0             | 5                             | 0.03                             | 0.81                       |
| Wolf + Preysz                                  | 158.0       | 4.0             | 4                             | 0.03                             | 0.81                       |
| Wolf + Slope + Forest                          | 158.0       | 4.0             | 5                             | 0.03                             | 0.81                       |
| Wolf + Preysz + TRI                            | 158.9       | 4.9             | 5                             | 0.02                             | 0.82                       |
| Wolf + Preysz + Elev                           | 159.1       | 5.1             | 5                             | 0.02                             | 0.80                       |
| Wolf + Preysz + Forest                         | 160.0       | 6.0             | 5                             | 0.01                             | 0.81                       |
| Wolf + Preysz + Season                         | 160.1       | 6.1             | 5                             | 0.01                             | 0.80                       |
| Wolf + Preysz + Slope + Forest + Elev + Season | 161.4       | 7.3             | 8                             | 0.01                             | 0.82                       |
| Wolf                                           | 162.3       | 8.3             | 3                             | 0.00                             | 0.77                       |
| Wolf + Forest                                  | 163.9       | 9.9             | 4                             | 0.00                             | 0.78                       |
| Wolf + Season                                  | 164.3       | 10.2            | 4                             | 0.00                             | 0.77                       |
| Wolf + Forest + Elev                           | 165.2       | 11.1            | 5                             | 0.00                             | 0.78                       |
| Wolf + Season + Elev                           | 165.6       | 11.6            | 5                             | 0.00                             | 0.77                       |
| Wolf + Forest + Season                         | 165.9       | 11.9            | 5                             | 0.00                             | 0.77                       |
| Preysz                                         | 173.2       | 19.2            | 3                             | 0.00                             | 0.68                       |
| Slope                                          | 177.4       | 23.4            | 3                             | 0.00                             | 0.65                       |
| Season                                         | 183.7       | 29.6            | 3                             | 0.00                             | 0.57                       |
| Forest                                         | 184.1       | 30.1            | 3                             | 0.00                             | 0.56                       |
| Intercept only (Null)                          | 184.1       | 30.1            | 3                             | 0.00                             | 0.50                       |

<sup>a</sup> Parameters: Wolf = number of wolf days within 90 meter radius of cache site; Preysz = prey size, large (adult elk) or small (elk calves, all other ungulates), small prey were the reference category; Slope = slope (degrees) at cache site; Season = winter (October–March) or summer (April–September), summer was the reference category; Elev = elevation; Roughness = topographic roughness index.

<sup>b</sup> Models with  $AICc = 0.0$  reflect the top model,  $AICc \leq 2.0$  reflect models that cannot be excluded from consideration.

<sup>c</sup> Number of parameters = number of variables plus 1 for intercept and 1 for error term.

<sup>d</sup>  $AICc$  weights.

<sup>e</sup> ROC AUC = Receiver Operating Characteristics Area under the Curve, an assessment of model fit (see chapter 3 for further explanation; Swets 1988; Manel et al. 2001; Boyce et al. 2002).

a cougar might be injured or killed while subduing prey (Hornocker 1970; Ross et al. 1995; Logan and Sweanor 2001; Murphy and Ruth 2010). Adult elk and other large-bodied prey presumably required more effort and time to manip-

ulate and kill and may have run greater distances (150–200 meters) than did smaller ungulate prey (10–15 meters; Laundré and Hernández 2003) before being successfully subdued and killed by cougars. Once killed, large prey were

**TABLE 7.5.** Influence of prey and landscape characteristics on the odds of a bear displacing a cougar from its kill on the Greater Yellowstone Northern Range, 1998–2005. Information-theoretic results for candidate logistic regression models used to assess a kill sample of 137 cougar-killed ungulates.

| <i>Model<sup>a</sup></i>                | <i>AICc</i> | $\Delta AICc^b$ | <i>Parameters<sup>c</sup></i> | <i>w<sub>i</sub><sup>d</sup></i> | <i>ROC AUC<sup>e</sup></i> |
|-----------------------------------------|-------------|-----------------|-------------------------------|----------------------------------|----------------------------|
| Season + Preysz + Carcass + Slope       | 144.3       | 0.0             | 6                             | 0.36                             | 0.80                       |
| Season + Preysz + Carcass               | 145.3       | 1.0             | 5                             | 0.22                             | 0.78                       |
| Season + Preysz + Carcass + Slope + TRI | 146.5       | 2.2             | 7                             | 0.12                             | 0.79                       |
| Season + Preysz + Carcass + TRI         | 146.6       | 2.3             | 6                             | 0.11                             | 0.77                       |
| Season + Preysz + Carcass + Elev        | 147.0       | 2.7             | 6                             | 0.09                             | 0.77                       |
| Season + Preysz + Carcass + Forest      | 147.5       | 3.2             | 6                             | 0.07                             | 0.78                       |
| Season + Carcass + Slope                | 150.1       | 5.8             | 5                             | 0.02                             | 0.77                       |
| Season + Preysz + Food + Slope          | 153.4       | 9.1             | 6                             | 0.00                             | 0.77                       |
| Season + Carcass                        | 153.8       | 9.5             | 4                             | 0.00                             | 0.73                       |
| Season + Preysz + Food                  | 154.4       | 10.1            | 5                             | 0.00                             | 0.76                       |
| Season + Preysz + Forest + Food         | 156.6       | 12.3            | 6                             | 0.00                             | 0.76                       |
| Season + Food                           | 159.1       | 14.8            | 4                             | 0.00                             | 0.72                       |
| Season + Preysz + Slope                 | 160.0       | 15.7            | 5                             | 0.00                             | 0.72                       |
| Season + Preysz + Food + Forest + Elev  | 161.9       | 17.6            | 7                             | 0.00                             | 0.68                       |
| Season + Preysz + WBP + Slope           | 162.1       | 17.8            | 6                             | 0.00                             | 0.72                       |
| Season + Preysz + WBP                   | 164.0       | 19.7            | 5                             | 0.00                             | 0.68                       |
| Season + Preysz + Forest                | 164.0       | 19.8            | 5                             | 0.00                             | 0.69                       |
| Preysz + Food                           | 164.1       | 19.9            | 4                             | 0.00                             | 0.66                       |
| Preysz                                  | 165.9       | 21.6            | 3                             | 0.00                             | 0.63                       |
| Preysz + Forest + Food                  | 166.2       | 21.9            | 5                             | 0.00                             | 0.66                       |
| Preysz + Carcass + Slope                | 166.3       | 22.0            | 5                             | 0.00                             | 0.66                       |
| Season + Prey                           | 166.3       | 22.0            | 4                             | 0.00                             | 0.63                       |
| Preysz + Carcass                        | 167.8       | 23.5            | 4                             | 0.00                             | 0.61                       |
| Preysz + Forest                         | 168.0       | 23.7            | 4                             | 0.00                             | 0.64                       |
| Season + Forest                         | 168.1       | 23.8            | 4                             | 0.00                             | 0.64                       |
| Intercept only (Null)                   | 171.1       | 26.8            | 6                             | 0.00                             | 0.50                       |
| Season                                  | 174.9       | 30.6            | 3                             | 0.00                             | 0.53                       |

<sup>a</sup> Variables: Preysz = large (adult elk) or small (all other ungulates); Forest = forested or nonforested site; Foods = combined standardized spring carcass counts/km and fall whitebark pine cone counts; Season = spring/summer (April–July) or fall (August–November); Slope = slope (degrees) at site; Carcass = spring carcass counts; WBP = fall whitebark pine cone counts; TRI = topographic roughness index.

<sup>b</sup> Number of parameters = number of variables plus 1 for intercept and 1 for error term.

<sup>c</sup> Number of parameters = number of variables plus 1 for intercept and 1 for error term.

<sup>d</sup> AICc weights.

<sup>e</sup> ROC AUC = Receiver Operating Characteristics Area under the Curve, an assessment of model fit (see chapter 3 for further explanation; Swets 1988; Manel et al. 2001; Boyce et al. 2002).

commonly left at the site of death in more open vegetation, apparently because they were difficult for cougars to move (Murphy and Ruth 2010).

We observed variation in the ability of cougars to conceal such kills with plucked hair, grass, and sagebrush (figs. 7.3 and 7.4). Small ungulate prey were more commonly killed in

forested cover or were dragged substantial distances to tree cover near steep cliff faces that provided security while cougars bedded (Ruth 2004b; Murphy and Ruth 2010).

Difficulties concealing large kills and the greater amount of time required to process and consume large prey (95 percent confidence interval of 2.8 to 5.7 days) did translate



**FIGURE 7.3.** Maternal female cougar F125 caching a bull elk killed in open grass-sage habitat on the Greater Yellowstone Northern Range. She is pulling “plucked hair” to cover the area where she has begun feeding in an attempt to conceal the kill from detection by scavengers. The following morning, a grizzly bear had taken over the carcass, and several wolves were bedded nearby. Photo by Dan Stahler, National Park Service.

to greater risks of detection and displacement for cougars (tables 7.6–7.9). Large prey comprised 38 percent of our kill sample and 70 percent of the displacements by wolves. A similar pattern existed for bears displacing cougars from kills of large prey—53 percent of displacements by bears occurred at large prey carcasses, yet our kill sample contained 33 percent large prey. The odds of wolves displacing

cougars were two and a half times greater (table 7.6) and the odds of bears displacing cougars were almost three times greater (table 7.7) for kills of large versus small ungulate prey. In one instance maternal female cougar F125 killed an adult elk in open sagebrush habitat (fig. 7.3). By the next morning, a grizzly bear had taken over the carcass, and several wolves were bedded nearby. Female F125 did not return.





**FIGURE 7.4.** Cow elk cached by cougar male M148 in open sagebrush near Hellroaring Creek. Although in the open, this carcass was better concealed in big sagebrush than the elk shown in figure 7.3. Male M148 bedded upslope in a rock outcrop several hundred meters from the kill. Photo by Jason Husseman, Hornocker Wildlife Institute/Wildlife Conservation Society.

### Wolf Activity

Cougars were less effective at concealing kills in areas of greater wolf use and at concealing large kills on lower slopes (fig. 7.5a, 7.5b). The odds that a cougar would be displaced from a kill were two times greater for every 1 percent increase in wolf use, and displacement was two times lower as slope increased by 10 degrees (table 7.6). Our index of wolf use did not account for the fact that wolf use varied across rugged and open terrain and on greater and lesser slopes. Yet it made sense that wolves tended to use less steep slopes while denning and during hunting, thereby encountering cougar kills on steeper slopes less often. On the Greater Yellowstone Northern Range, wolves made kills on slopes averaging 7 to 8 degrees. Moreover, large ungulate prey were more typically killed by cougars on gentler slopes (less than 17 degrees, on average) and in open areas (58 percent of kills) than were small ungulates. Therefore large ungulate kills occurred in areas of greater wolf use than did small ungulate kills (see table 5.6) [5]. Similarly, in Glacier National Park, Ruth (2004a) reported that wolves used slopes of less than 5 percent (3 degrees), whereas cougars were typically located on slopes averaging 15 percent (9 degrees) in summer.

**TABLE 7.6.** Cougars displaced from kills by wolves on the Greater Yellowstone Northern Range, 1998–2005: estimates of beta coefficients, standard error (in parentheses), and odds ratios (below beta coefficients) for parameters in the top logistic regression models ( $\Delta AIC_c \leq 2.0$ ).

| Model Rank | Ln (Wolf Days)     | 10° Slope           | Large Prey         | 100m Elev.         |
|------------|--------------------|---------------------|--------------------|--------------------|
| 1          | 0.88 (0.24)<br>2.4 | −0.65 (0.29)<br>0.5 | 0.91 (0.46)<br>2.5 | *                  |
| 2          | 0.95 (0.27)<br>2.6 | −0.63 (0.29)<br>0.5 | 0.91 (0.46)<br>2.5 | 0.09 (0.13)<br>1.1 |

**TABLE 7.7.** Cougars displaced from kills by bears on the Greater Yellowstone Northern Range, 1998–2005: estimates of beta coefficients, standard error (in parentheses), and odds ratios (below beta coefficients) for parameters in the top logistic regression models ( $\Delta AIC_c \leq 2.0$ ).

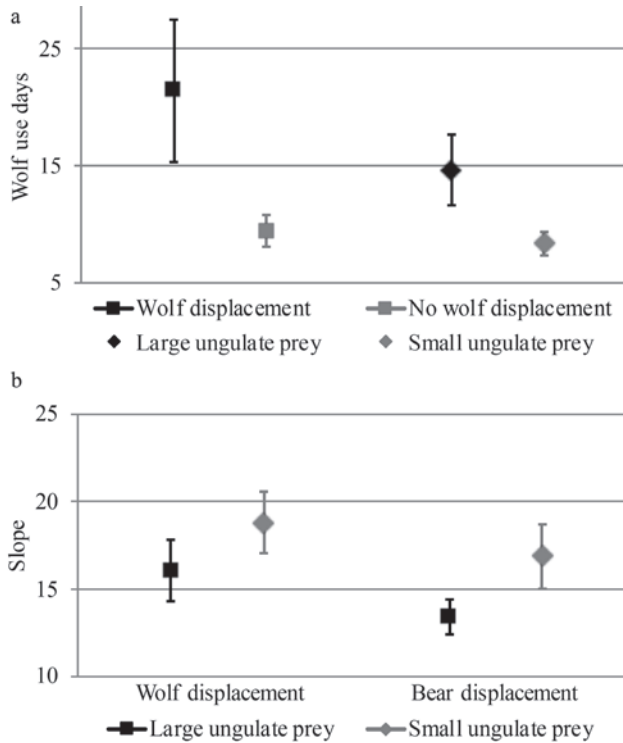
| Model Rank | Fall                 | Large Prey          | Carcass Count        | 10° Slope            |
|------------|----------------------|---------------------|----------------------|----------------------|
| 1          | −3.57 (0.79)<br>0.03 | 1.29 (0.47)<br>2.77 | −2.76 (0.76)<br>0.05 | −0.46 (0.29)<br>0.64 |
| 2          | −3.56 (0.78)<br>0.03 | 1.45 (0.46)<br>3.22 | −2.82 (0.76)<br>0.05 | *                    |

Chances of displacement by wolves increased when cougars made kills in winter and at lower elevations, but odds of displacement declined when kills were in forested areas (tables 7.4 and 7.6). Wolves detected 25 percent of cougar kills in winter compared to 17 percent in summer, and they displaced cougars from 9 percent of their kills during winter compared to 5 percent during summer. However, the odds of displacement were weaker for these characteristics compared to wolf use, slope, and prey size [6].

### Seasonal Foraging by Bears

Given that cougars remain in low-elevation habitats in early spring in the mountainous northwestern United States and western Canada (Seidensticker et al. 1973; Murphy 1983; Logan and Irwin 1985) and bears emerge from dens in search for food during this time, seasonal habitat use has important consequences for bear detection of cougar-killed prey and the odds of cougars being displaced. The odds that a bear would locate and displace a cougar from a kill were greater in spring and summer than in fall. Spring-summer kills made up 55 percent of our sample and 74 percent of the displacements by bears (table 7.7, fig. 7.6). This greater detection of cougar kills by bears during spring in northern Yellowstone was consistent with findings by Murphy and colleagues





**FIGURE 7.5.** Displacement of cougars from their kills was more frequent in areas of increased wolf use (a) and for large kills—typically on less steep slopes—compared to small kills (b).

(1998) in the pre-wolf study. Whereas larger prey increased the chances of displacement, a greater availability of winter-killed carcasses in the spring and cougar kills on steep slopes reduced the odds of bears displacing cougars from kills (table 7.7, fig. 7.5b) [7]. The overlap of cougars, wolves, and prey on low-elevation winter habitat equated to winter- and predator-killed carcasses of ungulates accumulating at lower elevations prior to spring green-up.

In our study during wolf restoration, grizzlies were the first to emerge from dens and were more frequent spring visitors to cougar kills than were black bears. Ungulates provided as much as one-half of the energy required by grizzly bears during the non-denning season, and Yellowstone grizzlies fed on ungulates more often than do most brown and grizzly bears elsewhere in North America (Mattson et al. 1991; Mattson 1997). Between 1985 and 1990, Green and colleagues (1997) reported that the probability of grizzly bear use of carcasses in the spring increased with the amount of edible biomass and elevation. The greater use of bison and

adult elk and almost no use of elk calves and deer supported their contention that slower depletion rates of larger carcasses were important to bears using carcasses. Black bears more often used carcasses later in the spring, and use by black bears increased with decreasing elevation (Green et al. 1997). Grizzly bears may also use carcasses as an important food source more than black bears do because they are competitively dominant over black bears (Schwartz et al. 2006a).

## FORAGING COSTS OF DISPLACEMENT

Prior to wolf restoration, displacements by bears did not appreciably increase the rate at which cougars killed again over the long term, probably because such events occurred infrequently and rarely in sequence (Murphy et al. 1998). As wolves were restored to the Greater Yellowstone Northern Range, wolves and bears displaced cougars at almost double the PW rate—at least one in five kills. Here we estimate kill rates with and without displacement using 122 kill intervals from fifteen cougars where we examined the kill within fourteen days.

Cougar kill rate, measured in kilograms of prey biomass per day, was roughly 11 to 26 kg/day higher when cougars were displaced by wolves or bears than when they were not displaced from a kill. As noted previously, there was a greater difference in kill rate when cougars were displaced from large kills than when they were displaced from small ungulate kills (fig. 7.7) [8]. When their kills were not detected by wolves or bears, cougars spent 2.8 to 5.7 days (95 percent confidence interval) feeding on adult and yearling elk and 2.3 to 3.6 days feeding on small ungulate prey. This translated to cougars spending about two days longer on large prey kills and one day longer on small prey kills when other carnivores did not displace them [9].

Cougars killed adult elk averaging 216 to 230 kilograms and small ungulate prey that averaged 70 to 94 kg. Cougars potentially lost anywhere from 97 to 122 kg of biomass from large prey and an average of 27.2 kg (95 percent confidence interval = 6.7 to 47.7 kg) of biomass from small ungulate prey, not accounting for losses to other scavengers (tables 7.8, 7.9, and 7.10). When averaged over kill sequences, the daily biomass cougars lost to bears prior to wolf restoration averaged 0.64 kg/day (range was 0 to 4.7 kg/day), which represented 17 percent to 26 percent of their daily requirement of kilograms of food (Murphy et al. 1998). After wolf restoration, cougars lost as little as 0.94 kg/day for small ungulate prey

**TABLE 7.8.** Wolf displacement of cougars from large and small ungulate prey on the Greater Yellowstone Northern Range, 1998–2005. All kills ( $n = 358$ ) site-searched within fourteen days are included in the wolf sample.

| Scavenge Type      | Winter   |             |            | Summer   |             |            |
|--------------------|----------|-------------|------------|----------|-------------|------------|
|                    | <i>n</i> | Kill Sample | Proportion | <i>n</i> | Kill Sample | Proportion |
| WOLF DETECTIONS    |          |             |            |          |             |            |
| Small prey         | 30       | 150         | 0.20       | 11       | 81          | 0.14       |
| Large prey         | 31       | 85          | 0.36       | 10       | 42          | 0.24       |
| WOLF DISPLACEMENTS |          |             |            |          |             |            |
| Small prey         | 9        | 150         | 0.06       | 0        | 81          | 0          |
| Large prey         | 12       | 85          | 0.14       | 6        | 42          | 0.14       |

**TABLE 7.9.** Bear displacement of cougars from large and small ungulate prey on the Greater Yellowstone Northern Range, 1998–2005. Kills available to bears during spring, summer, and fall and kill sites searched within fourteen days are included in the bear sample ( $n = 190$ ).

| Scavenge Type      | Spring/Summer |             |            | Fall     |             |            |
|--------------------|---------------|-------------|------------|----------|-------------|------------|
|                    | <i>n</i>      | Kill Sample | Proportion | <i>n</i> | Kill Sample | Proportion |
| BEAR DETECTIONS    |               |             |            |          |             |            |
| Small prey         | 34            | 65          | 0.52       | 16       | 57          | 0.28       |
| Large prey         | 36            | 50          | 0.72       | 9        | 18          | 0.50       |
| BEAR DISPLACEMENTS |               |             |            |          |             |            |
| Small prey         | 13            | 65          | 0.20       | 7        | 57          | 0.12       |
| Large prey         | 18            | 50          | 0.36       | 4        | 18          | 0.22       |

to as much as 28 kg/day for large ungulate prey when they were displaced. These estimates reflect a loss of 20 percent to 100 percent of the daily kilograms of food required for individual cougars to meet their daily energy demands. Whereas at times such losses were substantial, the large variation in both studies probably reflects the sporadic nature of losses by cougars to competitors (Murphy et al. 1998).

Although solitary cougars may take longer to consume a carcass than do family groups, which could increase the odds of detection by competitors, maternal female cougars were displaced from kills (40 percent, 25 of 63 kills) more frequently than other social classes, although this difference was not statistically significant [10]. Male cougars were displaced (27 percent, 8 of 30 kills) as often as solitary females (25 percent, 7 of 28 kills). When we removed biases associated with sampling a greater number of maternal females, mothers supporting young remained somewhat more likely

to experience detection of and suffer displacement from their kills than were adult males and solitary females. While caring for growing offspring, female cougars killed more frequently than adult males and solitary females, translating to more carcasses on the landscape each year—roughly 56 to 68 per year per maternal female. Thus although family groups consumed kills more quickly, it was the frequency at which they killed that lent support to our prediction that kills of maternal females should be detected more frequently by competitors and scavengers.

Scavenging and displacement of cougars from their kills by wolves and bears is not unique to the Greater Yellowstone Northern Range. Wolf visits to cougar kills that potentially led to a meal ranged from 18 percent to 33 percent in the central Idaho wilderness and Glacier and Banff National Parks—wolves directly displaced cougars from 14 percent of their kills in Banff—all during winter (Kunkel et al. 1999; Ruth 2004a; Akenson et al. 2005; Kortello et al. 2007). Near Glacier National Park, grizzly bears and black bears visited 15 percent of cougar kills, and cougars lost at least half (four of eight) of these carcasses—primarily to grizzly bears that were active outside dens in winter (Ruth and Gniadek 1996; Murphy et al. 1998; Ruth 2004a). Because the frequency and outcome of interference competition between carnivorous competitors is extremely difficult to quantify, it is likely underestimated in most systems (Creel and Creel 2002).

## ADAPTATIONS AND BEHAVIORAL MECHANISMS OF SCAVENGERS

Scavenging is a flexible and opportunistic foraging strategy that allows many species to take advantage of food when encountered while avoiding risks associated with hunting and capture of large prey (Ross et al. 1995; Logan and Sweanor 2001; DeVault et al. 2003; Bauer et al. 2005; Knopff et al. 2010a). The adaptations and abilities of carnivores and scavengers to locate and exploit carrion likely contribute to asymmetry in which species succeed in detecting foraging opportunities and which species dominate during direct interactions (Murphy et al. 1998). Specifically, some species should have advantages over others based on their visual and olfactory abilities as well as their ability to cover ground quickly during a day.

Although it was clear that cougars were more likely to be displaced from a kill by wolves as wolf use increased, we did not have comparable data to evaluate whether displacement by bears was greater in areas of greater bear use. Yet based on



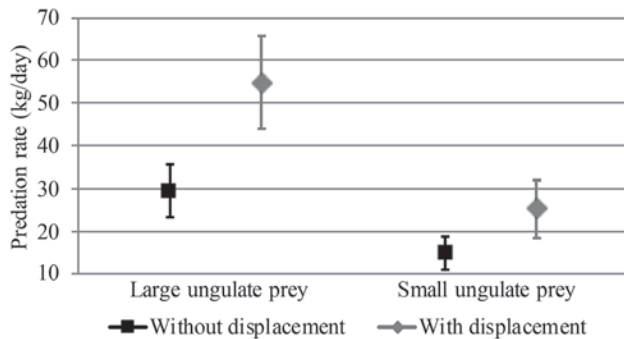
**FIGURE 7.6.** While ravens wait their turn, wolves approach a black bear guarding an elk that was killed and cached by a cougar. Photo by Daniel Stahler, National Park Service.

percentage of visits, bears were more effective than wolves at detecting cougar kills. How quickly bears, wolves, and other scavengers locate kills is surely influenced by the direction and intensity of wind, temperatures that assist or retard decomposition and distribution of odors, and arrival of avian scavengers. Although covering kills inhibits dissemination of odors, carcasses remain exposed to air currents while cougars feed (see Bischoff-Mattson and Mattson 2009). The marginally quicker arrival by bears at cougar kills than by wolves—about 1.9 days for bears and 2.3 days for wolves—

could be related to bears' refined olfaction and the increased odor emanating from kills in warmer temperatures compared to winter. In one instance GPS-collared cougar female F125 was displaced by a bear within four to six hours after she killed an elk calf in forested terrain. Such rapid olfactory detection of carcasses may give bears a competitive edge over other species in utilizing carrion.

Unlike wolves that chased cougars and did not always feed on kills, when bears arrived and displaced cougars from kills, they appeared dedicated to consuming what remained





**FIGURE 7.7.** Comparison of cougar predation rate for kills of large and small ungulates with and without displacement by wolves or bears on the Greater Yellowstone Northern Range, 1998–2005. Kill rates increased as a result of displacement from both large ( $P = 0.001$ ) and small ungulate prey ( $P = 0.001$ ).

of the carcass. As detection of carcasses can reward bears with large caloric benefit (Murphy et al. 1998), some individuals may learn to follow cougars and wolves from one kill to the next. For example, during our predation sequence monitoring of maternal female F107 in November 2000, a grizzly bear encountered her tracks and followed them to where F107 had gone to retrieve her kittens. The bear continued to follow her tracks as she took her kittens to feed at a kill she had made. After scavenging from that kill, the bear continued to follow the cougar tracks for over 1 kilometer. In the North Fork of the Flathead River, Montana, grizzly bears that were active outside dens during winter similarly followed cougars from one kill to another (Ruth and Gniadek 1996; Ruth 2004a).

Both bears and wolves have large daily activity radii—1.1 to 1.5 km for grizzly bears—but social search and hunting patterns and cursorial adaptations that enhance coverage of territories perhaps give canids an edge over some competitors in encountering and detecting carcasses (Mech and Boitani 2003a). We assumed that wolves generally encountered kills opportunistically during their travel throughout their home range. When wolves displaced cougars from kills, we observed variation in whether they consumed carcass remains, only partially fed on the carcass, or simply chased the cougar away, leaving the carcass untouched (fig. 7.8). As their behavior was less predictable than that of bears, wolves potentially posed greater risk to cougars and appeared more likely to give chase regardless of interest in a meal.

**TABLE 7.10.** Mean (95 percent confidence interval) foraging days and kilograms of biomass cougars lost when displaced from large (adult elk) and small ungulate prey on the Greater Yellowstone Northern Range, 1998–2005.

| Prey Size | Foraging Days Lost  |                     | Kg of Biomass/Day Lost  |                          |
|-----------|---------------------|---------------------|-------------------------|--------------------------|
|           | Wolves (n = 21)     | Bears (n = 29)      | Wolves (n = 21)         | Bears (n = 29)           |
| Large     | 1.77 (0.32 to 3.23) | 2.39 (0.94 to 3.84) | 96.69 (17.48 to 175.91) | 122.37 (47.95 to 196.78) |
| Small     | 0.86 (0.21 to 1.51) | 0.97 (0.32 to 1.62) | 27.20 (6.68 to 47.72)   | 22.80 (7.56 to 38.04)    |

Note: Cougars spent an average of 4.2 (2.8 to 5.7) days feeding on large kills and 2.9 (2.3 to 3.6) days feeding on small kills when their kills were not detected ( $n = 47$ ) by wolves or bears. Means for days and kilograms are at 95 percent confidence intervals.

Avian scavengers show morphological and behavioral adaptations for locating and exploiting carcasses efficiently—soaring flight, visual acuity, social foraging, recruitment of conspecifics to carcasses, and information sharing or association with large predators (Heinrich 1988, 1989; Heinrich et al. 1993; Stahler et al. 2002; Wilmers et al. 2003a). Although various avian scavengers were frequent visitors to a substantial proportion of cougar kills, we suspected that magpies and ravens acquired relatively large benefit from cougar-killed prey—especially adult elk killed in open areas. Magpies and jays more readily located kills made in forested habitats and thus may be the first to arrive at cougar kills in dense vegetation (see Selva et al. 2005); in forested sites they also avoid some competition with ravens. Flocks of ravens have been observed as more frequent visitors to carcasses located in open areas, and they associate more strongly with gray wolves than with cougars as a winter foraging strategy (Stahler et al. 2002; Selva et al. 2005). The vocal recruitment behavior of both ravens and magpies enhanced detection of cougar kills and other carcasses on the Greater Yellowstone landscape by wolves and other scavengers.

Even though cougars occasionally scavenge kills of other cougars or carcasses of animals that have died of natural and human causes (e.g., discarded parts of hunter kills or road-kill mammals; Ross and Jalkotzy 1996; Logan and Sweanor 2001; Bauer et al. 2005; Mattson et al. 2007; Knopff et al. 2010a), we documented few instances where Greater Yellowstone adult cougars scavenged (Murphy 1998). Scavenging by cougars appeared similarly infrequent prior to and during wolf restoration. The cougar's poor olfaction and mobility relative to other carnivores means that cougars may not discover





**FIGURE 7.8.** Wolf (upper left) and cougar kitten tracks in snow. These wolves located a kill made by the family group and followed the cougars, but the family group had sought refuge in cliffs on the steep slopes above the Yellowstone River and successfully evaded the wolves. Photo by Jason Husseman, Hornocker Wildlife Institute/Wildlife Conservation Society.

carriion as efficiently as do canids and ursids; in turn, there is increased potential that their kills will be quickly intruded upon. Only once did we document an adult male cougar scavenging from a wolf kill, five days after wolves had made the kill. As we discuss later, cougars may be able to make fine distinctions among risks associated with various predators, competitors, and conspecifics (Curio 1993; Lima and Steury 2005). We hypothesize that scavenging in proximity to numerous dangerous competitors, combined with low foraging returns associated with many carcasses, makes it a risky undertaking for cougars in systems with multiple large competitors.

When scavenging did occur, adult male cougars more commonly scavenged from and displaced other cougars from their kills (Ruth et al. 2010). During wolf restoration, adult male cougars displaced other males on three occasions and adult females twice. The body size of adult males may have provided advantages for them to take risks associated with scavenging. While we lacked data to examine any patterns, male cougars possibly detected other males at kills while exploring territories and perhaps sought out females at kills during peak mating seasons, as both of these occurred during our study.

The degree of scavenging may be greater than is thought from early studies, but because it is a *facultative* behavior, it

is likely highly variable and dependent upon conditions within various systems (Ross and Jalkotzy 1996; Murphy 1998; Logan and Sweanor 2001; Bauer et al. 2005; Mattson et al. 2007; Knopff et al. 2010a). Scavenging may be particularly beneficial for cougars and thus more common in areas where (1) large competitors are less abundant or absent, and (2) large prey occur at low density. In such environments foraging returns would outweigh risks, and calories gained through scavenging would extend search time when seeking out low-density prey. In fact, scavenging appears to occur more frequently in arid southwestern states, where large competitors are few and large prey occur at lower densities than in temperate northern landscapes (Murphy 1998; Logan and Sweanor 2001; Bauer et al. 2005; Mattson et al. 2007). Male cougars may more consistently take advantage of food when encountered, as they also scavenged more often than females in New Mexico and Southern California (Logan and Sweanor 2001; Bauer et al. 2005). An exception was widespread scavenging across sex-age classes of healthy cougars found by Knopff and colleagues (2010b) in the mountains, foothills, and agricultural lands east of Banff and Jasper National Parks, Alberta. Here, adult female cougars scavenged more frequently than adult males, and subadults scavenged approximately four times more frequently than adults, again highlighting the variation of characteristics in the complement of prey and predators in the system (Knopff et al. 2010a, 2010b). In contrast, whereas subduing and killing large prey can be hazardous, approaching carcasses of unknown source to scavenge may exceed risks of capturing prey on the Greater Yellowstone Northern Range. Despite a 50 percent decrease in elk counts from 1995 to 2005, elk remained an abundant source of prey (7–8 elk/km<sup>2</sup>; White and Garrott 2005) and, excluding bears, elk outnumbered carnivores by almost 227:1 in 1999 and 80:1 by 2003. Wolves outnumbered cougars by 2.5:1 averaged over the first two years of our study and by roughly 7:1 during the last two years of our study.

## STRATEGIES OF CARNIVORES FORAGING IN RISKY ENVIRONMENTS

Loss of a meal and risk of injury or death represent selective pressures for all large carnivores, and morphological and behavioral adaptations to reduce such encounters have been selected for in cougars and other carnivorous species. Size, forming social groups or remaining solitary, concealing kills, and abandoning carcasses when risks outweigh gains are a

few of the adaptations that enable carnivores to forage successfully when living among other large competitors.

### **Carnivore Size and Forming Social Groups**

For carnivores that outweigh their opponents, the problem of defending a large meal appears to be solved simply by being large, with fewer selective pressures to avoid risks from smaller scavengers or competitors. While there may be rare events when defense of food from conspecifics is necessary, site abandonment may be a simple strategy to avoid such conflict. Although they typically dominate at kill sites, grizzly bears do cover carrion under a mound of dirt and debris and bed next to or directly on top of carcasses they kill or have kleptoparasitized from other animals (Elgmork 1982; Smith and Bangs 2009). Such caching may primarily help reduce competition with microbes and arthropods, but it also helps conceal the carcass from various scavengers (Bischoff-Mattson and Mattson 2009). Tigers, a large and dominant carnivore in the Russian Far East, do not conceal their kills or their feces, as any carnivore seeking to scavenge from tiger kills must weigh high risk of injury or death (J. Goodrich, *Panthera*, pers. comm., September 24, 2013).

Forming social groups is another strategy that can be advantageous for defense against competitors and scavengers, to increase foraging proficiency, or both (Bertram 1978; Janson and Goldsmith 1995; Clutton-Brock et al. 1999; Heithaus and Dill 2002; Vucetich et al. 2004). Wolves, African wild dogs, African lions, and hyenas tend to eat large prey, are thus vulnerable to scavenging, and may minimize losses by foraging socially (Packer et al. 1990; Cooper 1991; Fanshawe and Fitzgibbons 1993; Gorman et al. 1998; Creel and Creel 2002). Larger groups are also better able to form defense against interlopers and lose less biomass to scavengers compared to smaller groups or singletons (Vucetich et al. 2004; Metz et al. 2011). The benefits of social groups outweigh the costs of increased hunting efforts and increased food sharing among group members (Vucetich et al. 2004).

### **Solitary Strategies and Carcass Concealment**

If defense of kills is a benefit of grouping, why, then, do cougars not adopt grouping behavior as a defense mechanism, as in prides of African lions or coalitions of cheetahs? For one thing, solitary living provides greater food benefit per individual compared to group living. And as previously mentioned, group living provides defense benefits, but a large

congregation more quickly draws attention to the point that competitor numbers can have an impact on the foraging success of subordinate carnivore groups (Bertram 1978; Packer et al. 1990; Janson and Goldsmith 1995; Creel and Creel 2002; Heithaus and Dill 2002).

While feeding alone reduces detection, it may be less effective in more open habitats, where frequent displacement by scavengers and competitors appears to have selected for more elaborate caching behavior. If cougar kills were detected more quickly—as is experienced by leopards in open savannah where detection can occur within minutes (Bailey 1993)—then selective pressures might have been strong enough for cougars to adopt tree-caching behavior. To avoid multiple dominant competitors, leopards climb trees, pulling up prey carcasses and draping them in trees so they can feed safely (Bailey 1993). Instead, forested habitats enabled cougars to adopt strategies to conceal kills in dense vegetation, move carcasses to cover, and cache prey under debris rather than to defend kills in large groups or cache kills in trees. When kills were mostly concealed in dense cover and covered, thereby reducing dissemination of odors, carcasses were generally not detected in most environments for several days (Beier et al. 1995; Bank and Franklin 1998; Bischoff-Mattson and Mattson 2009; Murphy and Ruth 2010). Burying feces in toilets at kill sites may further reduce detection of carcasses by competitors and other cougars (Logan and Sweanor 2001).

As our DW study progressed, we hoped to gain a better understanding of cougar behavior at kills and how frequently scavengers gained access to kills. From January through March 2002, field biologist Daniel Stahler conducted a pilot study with the objective of observing cougars on fresh kills. As a result of the difficulty of finding cougar kills that could be observed repeatedly from a location and where observation did not affect the behavior of cougars and scavengers present, only three kill sites were monitored for cougar-scavenger interactions. The total time spent observing these three kill sites was 1,165 minutes during the day, throughout which the attending cougars (F47 for two cow elk kills, F117 for one mule deer doe kill) were visible for 835 minutes, or 71.6 percent of the time. Only 22 minutes of observations involved cougars feeding during the day, whereas the remaining 813 minutes of observed cougar behavior at kill sites included sleeping, resting alert at the cache, grooming, or traveling in and out of the area.

Foraging success of scavengers at cougar-killed ungulate carcasses on the Greater Yellowstone Northern Range appeared restricted to (1) access to partially cached or uncovered carcasses while the cougar was not in the immediate area, particularly kills in open vegetation; (2) total abandonment by the cougar after three to five days, at which time carcasses were typically left uncovered; and (3) displacement by a dominant carnivore. While the attending cougar was in the immediate area, magpies, ravens, and golden eagles were the main scavengers present at each kill site (for 85.2%, 41.2%, and 8.2% of the total time, respectively). When cougars were in the immediate area of the kill, magpies were the most successful scavenger, with an average of five magpies (one-fourteen individuals) feeding for a total of 275 minutes on partially cached or uncovered carcasses.

Initial evidence from this pilot study indicated that cougars' behavior of hiding and caching ungulate carcasses, as well as bedding nearby and maintaining view of their kills, remained a successful strategy to limit avian and small mammalian scavenger access (through both physical and behavioral mechanisms) for kills cached in tree cover, despite scavenger discovery of kills. No scavengers fed while a cougar was bedded near the carcass, and vigilant cougars were seen hissing at magpies and ravens flying low overhead. On seven occasions we observed cougars jump at ravens flying over the kill and otherwise defend kills by killing coyotes, a fox, and a golden eagle that scavenged at kills. Between feeding bouts cougars generally bedded on the same slope or upslope at 85 percent of their kills and typically within 1.5 to 15 meters (95 percent confidence interval) from the kill ( $n = 179$  kills)—usually small ungulate prey. Cougars bedded slightly farther away from kills—9 to 33 meters (95 percent confidence interval)—when they bedded downslope from kills ( $n = 30$  kills), and such bed sites were generally situated in rock outcrop or cliffs. Secure bedding habitat next to a kill appeared less available in open habitats, as cougars typically bedded at a greater distance from these kills—sometimes as far as 200 meters from kills—and active defense may have been less achievable. The cats more commonly dragged smaller prey from more open habitat to tree cover near steep cliff faces (fig. 7.9).

Although large prey were more difficult than small prey for cougars to conceal, we found no evidence of cougars failing to cache prey during our study. Even with cooler temperatures or lack of sufficient debris for effective covering, cougars always attempted to cover their prey when not feed-

ing and prior to departing from the carcass. Where few large competitors are present, caching may not be as stereotypical a behavior, yet it still retains the purpose of reducing losses of edible tissue. Cougars in Arizona tended to relocate or bury kills more often in hotter temperatures and at lower elevations and less often at higher elevations (Bischoff-Mattson and Mattson 2009). The imperative for cougars to cache prey in our study compared to the findings in Arizona lends support to the hypothesis that selective pressures favor concealing carcasses when foraging solitarily in areas dominated by large competitors.

The size and number of competitors in an area exerting greater or lesser pressure as a selective force might also play a role. In Wilpattu National Park, Sri Lanka, leopards are the largest predator, rarely placing their kills in trees and instead feeding on carcasses in cover (Bailey 1993), similar to cougars. Lastly, unlike in African systems where competitors are not adapted to climbing trees, tree caching could prove an unsuccessful strategy in protecting kills from black bears and jaguars, which can climb. Even in areas of high carnivore use on the Greater Yellowstone Northern Range, terrain features such as steep slopes and rough topography hindered wolf or bear discovery of cougar kills and allowed kills to remain undetected. Retained through thousands of years, the concealment behaviors of cougars have proven largely successful at minimizing detection and loss of carcasses to competitors. When successful, they reap benefits because they do not share, and solitary living in complex habitat has remained adaptive.

### Carcass Abandonment

Animals of all kinds have little trouble perceiving changes in risks, making fine distinctions among risks associated with various predators and competitors, and they retain the ability to do so even for a long (multigenerational) period of no contact with predators (Curio 1993; Lima and Steury 2005). Greater Yellowstone cougars guarded carcasses from avian and smaller mammalian scavengers, yet they readily abandoned carcasses when large competitors, including humans, approached. Interestingly, if competitors departed within one to two days, cougars were likely to return and check on a carcass. This applied particularly for females with kittens. While it was risky to remain at and guard carcasses when competitors arrived, cougars appeared to be able to assess risks of returning for low-value carcass remains rather than proceeding to hunt again (Wilmers et al. 2003a; Elbroch and



Wittmer 2013). Perhaps cougars have retained or acquired knowledge that when they are actively displaced from their own kills, competitors will eventually leave. Thus the risks of returning to one's own kill in hope of acquiring remaining calories are less than those associated with scavenging unfamiliar kills, as detailed earlier.

## CHANGES IN THE SYSTEM

Following their restoration, the frequency at which wolves killed ungulate prey altered the pattern of carcass availability on the Greater Yellowstone Northern Range. Like cougars, wolves made kills year-round, and their presence provided a temporal subsidy to scavengers—supplementing that provided by cougars in more complex terrain—as carrion became more available year-round (Wilmers et al. 2003a). In early spring grizzlies followed wolf packs and took advantage of their kills—dominating wolves at carcasses about 80 percent of the time (Smith and Bangs 2009). Why, then, were bear displacements of cougar kills greater after wolf restoration and not similar or less? A greater frequency of displacements by bears during our wolf restoration study was likely related to an increase in the number of grizzly bears between the two study periods (Schwartz et al. 2006b). In addition, grizzly bear reliance on carrion had perhaps increased as a result of more consistent availability of carcasses from wolves coupled with a decline in other bear foods, particularly whitebark pine seed crops (M. Haroldson, US Geological Survey, pers. comm., July 2001). Whether carrion resulted from severe winters or wolf predation, an abundance of carcasses in the spring was to the cougar's advantage, as greater carcass availability moderated displacements by bears. Overall, rate of displacement of DW cougars was perhaps most strongly influenced by a greater proportion of large prey killed as the calf:cow ratio trended toward fewer calves and by somewhat milder winters, resulting in lower numbers of carcasses available during spring of 2000 through 2004. Ultimately, the frequency of displacements and large losses of biomass to competitors and scavengers year-round could further increase under changing climate or with reduced whitebark pine seed production, potentially altering rates of survival and successful rearing of offspring. We discuss this topic further in chapter 18.

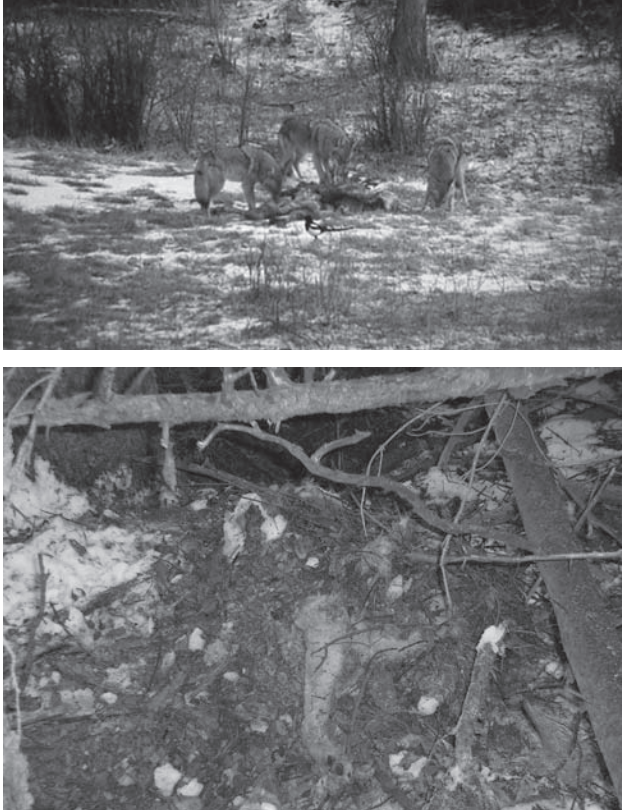
Whereas subordinate carnivores like cougars suffer losses when displaced, frequent scavenging by wolves may reduce the frequency with which wolves kill elk; and intraguild predation, where one carnivore kills another, may also stabi-



**FIGURE 7.9.** During a flight in July 2002, pilot Doug Chapman observed cougar female F125 killing a pronghorn at the edge of a small meadow around noon. When we later investigated the site, which was within an area frequented by bears and the Leopold wolf pack, we tracked along a path of pronghorn hair left along a 200 meter path as F125 moved the carcass from where she killed it to a more secure area near cliffs above the Yellowstone River on the Greater Yellowstone Northern Range. For two days F125 and her two kittens bedded in and near the rocky cliffs below the carcass between bouts of feeding on the pronghorn. Photo by Polly Buotte, Hornocker Wildlife Institute/Wildlife Conservation Society.

lize mesocarnivore populations (Smith et al. 2008). During winter in particular, carcasses were an important food source for smaller carnivores (fig. 7.10a; Merkle et al. 2009). Coyotes and foxes were sometimes killed by cougars while attempting to scavenge at carcasses that were still attended by cougars, but this occurred infrequently compared to the deaths coyotes suffered from wolves (fig 7.10b). The result of interactions between wolves and coyotes has been a 39 per-





**FIGURE 7.10.** Coyotes and other small carnivores benefit from scavenging carcasses during winter (a), but they face great risks and are often killed by wolves and less frequently by cougars while scavenging wolf- or cougar-killed prey. Compared to other cougars, resident female F47 showed a particular affinity for ambushing coyotes at kills as well as away from kills. After sitting by a tree along the edge of the frozen Lamar River and observing coyotes on the river ice, she crept several hundred meters across the frozen river, ambushed one coyote in the group, dragged it back to the cover of trees, fed, and then cached it (b). On another occasion, female F47 stashed her young kittens, traveled across Slough Creek, and lay low in a small outcrop of rocks next to a recently abandoned wolf kill. The following day she remained there with her kittens. Our investigation of the site revealed that she had not scavenged the wolf kill but instead had ambushed coyotes that were scavenging at the abandoned kill.

cent decrease in coyote abundance in northern Yellowstone (Crabtree and Sheldon 1999; Berger and Gese 2007). Substantial reductions in the density of other carnivores as a result of this intraguild predation may moderate the effect of food stealing. Thus these complex interactions at kills may at times “even out” or perhaps even stabilize the effects of multiple carnivores on ungulate prey.

## SUMMARY

Although they are ephemeral, carcasses tend to draw attention from many species that then directly interact and compete for a meal. Similar to what has been observed for wolf kills in Yellowstone, six avian and six mammalian species visited and potentially gained foraging benefits from at least 62 percent of the cougar kills we documented. Wolves and bears were the only species capable of dominating cougars and displacing them from their kills. Wolves visited one in four cougar kills and displaced cougars from at least one in thirteen kills, mostly in winter. Bears visited one in two cougar kills and displaced cougars from at least one in five kills—

almost twice the rate recorded prior to wolf restoration and over twice the rate at which wolves displaced cougars. Displacement by wolves was most likely during winter and in areas that wolves used most frequently. Bears displaced cougars in spring and summer more than in fall. The greater number of carcasses available in the spring—whether winter kills, wolf kills, or both—benefited cougars, as it decreased the odds of displacement by bears.

For cougars, the risks associated with killing adult elk and other large-bodied prey extend beyond those associated with pursuit and capture. The longer time spent feeding at large kills than at small kills, combined with greater visibility of these kills to avian and mammalian scavengers, translated to greater risks of displacement for cougars. Large prey tended to be killed by cougars on less steep slopes in open areas, which were areas with greater wolf use and also of enhanced detection of carcasses by bears. Even in areas of high carnivore use, terrain features such as steep slopes and rough topography may hinder wolf or bear discovery of cougar kills and enable kills to remain undetected.

When not displaced by competitors, cougars spent two days longer feeding on large ungulate prey kills and one day longer feeding on small ungulate prey. When cougars were displaced by wolves or bears, kill rates increased by roughly 11 to 26 kilograms of ungulate biomass per day above their rate of killing when they were not displaced. Cougars lost as little as 0.94 kg/day of ungulate biomass for small ungulate prey to as much as 28 kg/day for large ungulate prey—or 20

percent to 100 percent of their daily energy requirements—when they were displaced from kills. Although their kills are frequently detected in the complex habitat of the Greater Yellowstone Northern Range, concealment of kills—dragging carcasses to dense vegetation and covering them with debris—remained an adaptive behavior effective for this solitary felid in minimizing detection and reducing loss of carcasses to competitors.

## CHAPTER 8

### Combined Influences

#### *Cougars, Wolves, and Humans*

Elk and other ungulate species are widely distributed and migrate across a mosaic of landscapes with different land ownership and management policies and where human recreational and agricultural uses vary. Consequently, although national parks are managed to minimize human impacts, they typically are not insulated from differing agency management goals or expectations of different segments of the public (Woodroffe 2001; Ruth et al. 2003; Hamlin et al. 2009b). The arrival of wolves and the decline of elk have made northern Yellowstone an area of intense interest, debate, and research.

On the Northern Range and in an increasing number of areas, cougar predation is overlain on bear and wolf predation, but we were not aware of studies that have assessed the fluctuating role of predation by all three large carnivores. In areas with high wolf and grizzly bear to prey ratios, including the northern Yellowstone, Gallatin Canyon, and Madison-Firehole winter ranges, elk numbers have declined substantially since wolf restoration, while in other areas elk numbers have remained stable or increased since wolf restoration began (Hamlin et al. 2009a, 2009b). Although these events coincide with PW and DW periods, other potentially influencing factors have also varied in these areas along with increases in wolf numbers, such as increased drought and increased numbers of grizzly bears. Teasing out the effects of multiple predators on prey is additionally challenging because human hunting is present in most studied ungulate populations, and changing snow and summer forage conditions act in a synergistic manner to influence carnivore-prey interactions. In the following sections we examine where cougar predation fits into the picture of factors that affect elk. We examine the offtake of prey by cougars relative to wolves, bears, and human hunters and address whether cougar pre-

dition was additive or compensatory to these other sources of offtake. We also examine whether cougar predation significantly limited the population of elk and mule deer prior to and during wolf restoration as influenced by the relative ratio of carnivores to prey.

#### **DETERMINING OFFTAKE OF ELK BY COUGARS, WOLVES, AND HUNTERS**

In their 2009 report, Hamlin and colleagues (2009a) estimated preseason elk numbers by adjusting counts of elk. They adjusted aerial survey counts with sightability models, observability estimates, population modeling, and hunter harvest from Montana Fish, Wildlife and Parks annual harvest surveys for elk (Singer et al. 1997; Hamlin and Ross 2002). They also determined the proportion of elk removed by hunters and wolves each year during the PW period of 1985 through 1994–1995 and the DW years of 1997 through 2007–8. Instead of introducing additional estimates and rates of offtake, we use those of Hamlin and colleagues (2009a: 76, appendix table 1) for elk abundance and wolf and hunter offtake. However, we include an important breakout of calves when comparing the proportion of elk removed by cougars, wolves, and hunters each year. Hamlin and co-workers (2009a) defined winter—November through April—and summer the same way we did. The rate at which wolves killed elk changed between early and late winter, and those rates were applied to the corresponding winter months, but a conservative wolf kill rate of 50 percent of the winter rate was applied for the summer period of May through October (Smith et al. 2004a, 2004b, 2005, 2006, 2007, 2008; Hamlin et al. 2009a). We used wolf selection of elk during winter to partition offtake by wolves into sex-age classes of elk—bulls, cows, and calves.

Prior to wolf restoration, Murphy (1998) estimated the total predation rate of elk and mule deer by cougars for 1987 through 1991–92. Although he used sightability and hunter-harvest–adjusted elk counts, elk abundance estimates differed slightly from those of Hamlin and colleagues (2009a) because of the time period for which estimates were calculated—June of one year to May of the following year for Murphy (1998) and October 15 to October 14 the following year for Hamlin and colleagues (2009a). We applied Murphy’s (1998) estimates of offtake by cougars for the PW period. Following these methods, we averaged summer and winter kill rates of cougars during wolf restoration—because they did not differ significantly—for each social class of cougars. We used cougar selection of elk to partition offtake into sex-age classes of elk—bulls, cows, and calves. We applied these total predation rate values by social class to the minimum estimated number of cougars within each social class during each year of our study. So that the higher kill rate of maternal females was incorporated in annual estimates, we applied the annual proportion of adult female cougars that were supporting offspring each year to estimated numbers of female cougars each year.

The growth of the elk population hinged most strongly on the survival of adult elk, which may have at least twice the effect on population growth compared to neonatal survival (Gaillard et al. 1998; Eberhardt 2002; Smith et al. 2006; Raithel et al. 2007; Garrott et al. 2009b). However, once elk calves survived their first winter, their survival rates were generally high and constant, and they potentially added to population growth if adult survival remained high or they replaced adults that died (Hamlin and Ross 2002). For instance, annual mortality of 20 percent of adult female elk required annual recruitment of 34 calves per 100 cows to maintain stability in an elk population, assuming an even sex ratio of calves (Evans et al. 2006). Young of the year ungulates were critical as food for cougars and wolves and for female cougars provisioning offspring and also contributed to the growth of elk and deer populations (Hornocker 1970; Murphy 1998; Logan and Sweanor 2001; Peterson and Ciucci 2003). Because cougars, wolves, and bears focused predation on elk calves, metrics of the ratio of carnivores to adult elk and to calves may add to understanding the synergistic effects of multiple carnivores across systems.

Kill rate for obligate carnivores, such as cougars and wolves, appears fairly consistent over a wide range of prey densities,

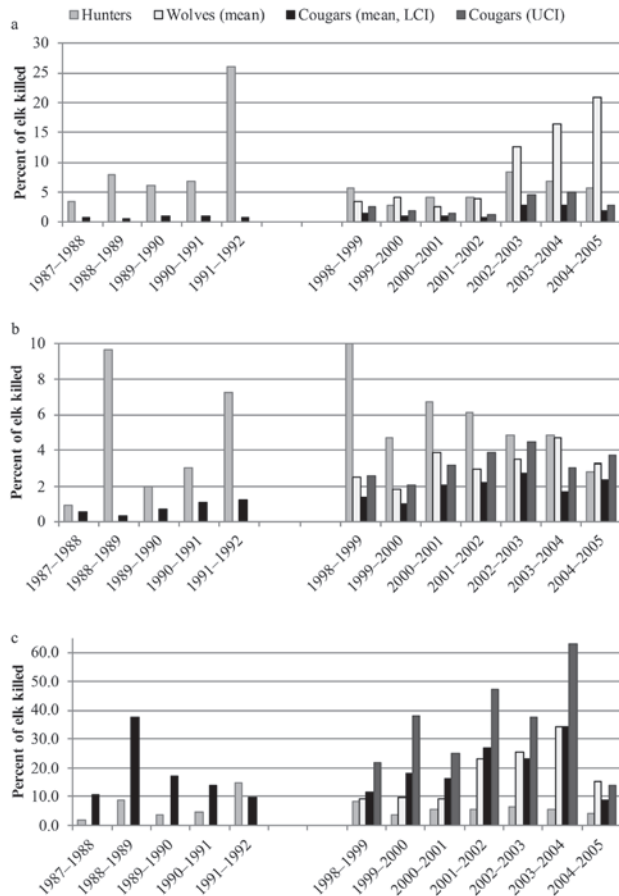
whereas the kill rate of facultative carnivores, such as bears and coyotes, may depend more on alternate food resources and prey density (Ballard et al. 2001). In comparing kill rates of Northern Range wolves with those of other wolves, Smith and colleagues (2004) found similar kill rates across years, even with large variation in prey density. Thus they found a lack of support for kill rates increasing with prey density (e.g., Type II functional response). Vucetich and colleagues (2011) found that total predation rate of wolves is better explained by the ratio of wolves to prey compared to using the per capita kill rates of wolves. We, too, found that although kill rates by Yellowstone cougars varied by cougar social class, the average kill rates within each social class remained relatively stable between two time frames—summer to winter and pre-wolf to during wolf restoration—even though prey abundance varied substantially. Subtler variation and influences on kill rates were apparent only when kill rates were broken down into handling time and movements made by cougars before making the next kill (see chapter 6; Murphy et al. 2011).

Factors suggesting that the ratio of carnivores to elk should have a strong influence on total predation rates are: (1) changing numbers of wolves, grizzly bears, and prey with sustained human harvest; (2) the differential vulnerability of age and sex classes of elk to both cougars and wolves; (3) competition for live prey and carcasses as influenced by prey size; and potentially (4) indirect effects of predation (e.g., *apparent competition*). Indeed, a ratio-dependent model is supported by other research (Eberhardt 2000; Becker et al. 2009b; Vucetich et al. 2011).

### **SYNERGISM OF RATIO-DEPENDENT INFLUENCES, CARNIVORE PREDATION, HUNTER HARVEST, AND DROUGHT**

Cougars typically have little numerical effect on their prey when predation losses are less than 5 percent annually (Murphy et al. 2011), and for large prey such as elk, cougar predation alone is therefore typically not strongly limiting where elk are the most abundant prey (Hornocker 1970; Murphy 1998; Murphy and Ruth 2010). With the exception of two years, 2002–2003 and 2003–2004, cougars removed less than 1 percent to 5 percent of adult Northern Range elk across all PW and DW years (fig. 8.1). Yet this predation was not evenly distributed across all elk age classes. Competitors and humans also contributed to offtake of various age classes from the elk population.





**FIGURE 8.1.** Estimated percentage of elk bulls (a), cows (b), and calves (c) killed annually by hunters, wolves, and cougars on the Greater Northern Yellowstone Range before wolf restoration, 1987–92, and with wolves present, 1998–2005. Hunter harvest estimates include crippling loss. Pre-wolf and during wolf cougar estimates are means that incorporate seasonal and cougar social class variation. Estimates shown for during wolf cougars are the lower (black bars; 1998–1999 through 2004–2005) and upper (dark gray bars; 1998–1999 through 2004–2005) 95 percent confidence interval (CI) around the mean. The lower and upper ends of cougar variation were not readily available at a 95 percent confidence interval (Murphy 1998; Hamlin and Ross 2002; Hamlin et al. 2009a).

### Offtake and Ratio-Dependent Influences Prior to Wolves

Despite a steady increase in PW cougar numbers, which grew at about 9 percent to 25 percent over the five-year period 1987 through 1991 (chapter 16; Newby et al. 2013), estimated numbers of elk and mule deer fluctuated at about

21,500 and 2,700, respectively, during that period. Cougars removed less than 2 percent of adult elk and 9 percent to 17 percent of calf elk, except for the year following the 1988 fires, when cougars removed almost 38 percent of calves because calf numbers plummeted following the drastic change in forage conditions.

During the PW period, grizzly bears outnumbered cougars by roughly 2.5:1. Only recently have kill rates been estimated for grizzly bears at 1 elk calf every  $4.3 \pm 2.7$  days and for black bears at 1 elk calf every  $8.0 \pm 4.0$  days during June (Singer et al. 1997; Barber-Meyer et al. 2008; Fortin et al. 2012). How these predation rates translate to offtake of calves has been estimated in two studies that assessed cause-specific mortality of elk calves: one prior to wolf restoration (Singer et al. 1997) and one following wolf colonization (Barber Meyer et al. 2008). Prior to wolf restoration, grizzly bears and coyotes accounted for 28 percent and 20 percent, respectively, of deaths caused by predators (Singer et al. 1997). While that study noted that cougars killed a single radio-collared calf, another suggested that cougar predation accounted for 2 percent to 4.4 percent of calf deaths between 1987 and 1990 of the PW period (Green et al. 1997).

During the PW period and including grizzly bears, the ratio of large carnivores to adult elk was 3–6 carnivores:1,000 adult elk. At this time, when the ratio of calves per 100 female elk was high, calves absorbed a substantial level of predation and buffered adult elk from predation by cougars. Numbers of cougars and bears ranged from 16–30 carnivores:1,000 calves between 1987 and 1991–1992, with the exception of after the 1988 fires, when calves plummeted and the ratio neared 50 cougars and bears per 1,000 calves (table 8.1). Yet enough calves remained alive—an average 1 to 9 calves to replace cows—to outpace losses of adult elk (table 8.1; Hamlin et al. 2009b).

Assuming that hunter numbers were roughly equal to the number of elk harvested each year, hunters outnumbered cougars and grizzly bears at a ratio ranging from 8:1 to 58:1 between 1987 and 1991–1992 (table 8.1). In the years preceding the arrival of wolves, hunters removed 3 percent to 26 percent of bull elk, 2 percent to 15 percent of calves, and 1 percent to 9 percent of cow elk—mainly prime-age cows of high reproductive value (fig. 8.1; Wright et al. 2006). Again assuming that hunter numbers were roughly equal to the number of elk harvested each year, the ratio of hunters to elk ranged from 23:1,000 elk to 200:1,000 elk (table 8.1).

**TABLE 8.1.** Ratio of calf elk:cow elk, carnivores:1,000 elk or elk calves, and cougars:other carnivores from estimated numbers of elk and carnivores on the Greater Yellowstone Northern Range, 1987–88 through 2004–5. Highlighted area indicates years when calf recruitment declined markedly and the ratio of carnivores to calves doubled to quadrupled.

| Year      | Calf:Cow <sup>a</sup> | Ratios                            |                  |                        |                         |             |
|-----------|-----------------------|-----------------------------------|------------------|------------------------|-------------------------|-------------|
|           |                       | Cougars + Wolves + Grizzly Bears: |                  | Hunters:               | Wolves + Grizzly Bears: | Hunters:    |
|           |                       | 1,000 Adult Elk                   | 1,000 Elk Calves | 1,000 Elk <sup>b</sup> | 1 Cougar <sup>c</sup>   | 1 Carnivore |
| 1987–88   | 23                    | 3.3                               | 17.4             | 23.1                   | 3                       | 8           |
| 1988–89   | 6                     | 2.6                               | 50.3             | 142.4                  | 3                       | 58          |
| 1989–90   | 19                    | 4.8                               | 30.2             | 44.4                   | 2                       | 11          |
| 1990–91   | 26                    | 5.6                               | 21.9             | 59.0                   | 2                       | 13          |
| 1991–92   | 44                    | 5.9                               | 16.3             | 199.7                  | 2                       | 46          |
| 1998–99   | 34                    | 12.1                              | 57.1             | 131.0                  | 6                       | 13          |
| 1999–2000 | 23                    | 10.0                              | 56.5             | 60.8                   | 5                       | 7           |
| 2000–2001 | 29                    | 12.2                              | 71.9             | 90.0                   | 6                       | 9           |
| 2001–2    | 14                    | 12.9                              | 142.0            | 85.6                   | 7                       | 7           |
| 2002–3    | 12                    | 18.0                              | 183.7            | 85.8                   | 7                       | 5           |
| 2003–4    | 12                    | 22.4                              | 234.7            | 81.4                   | 7                       | 4           |
| 2004–5    | 13                    | 18.1                              | 172.8            | 51.5                   | 11                      | 3           |

<sup>a</sup> Ratios are based on estimated numbers of carnivores including offspring (cougar kittens, wolf pups, bear cubs).

<sup>b</sup> Hunter numbers were assumed to equal those successful at killing elk, including crippling loss (numbers from Hamlin et al. 2009a).

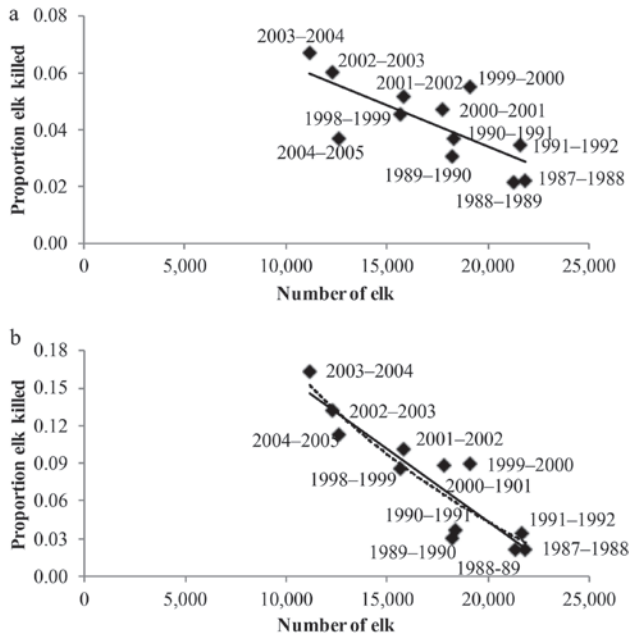
<sup>c</sup> Pre-wolf year ratios are grizzly bears per one cougar, as no wolves were present. Estimates of black bears were not available.

### Offtake and Ratio-Dependent Influences during Wolf Restoration

In the early years following wolf restoration, the cougar population initially continued to grow at upward of 10 percent between 1998 and 2001. During peak wolf and declining elk numbers in 2002 through the end of our study, the cougar population was in decline by as much as 13 percent to 22 percent (chapter 16). Yet the proportion of elk removed by cougars each year increased as a direct result of declining elk numbers and declining availability of calves. Consequently, cougar predation on calves during wolf restoration became more substantial—ranging from 4 percent to 24 percent annually above losses caused by wolves and hunters combined (fig. 8.1). During this period the rate of mortality cougars contributed to the elk population each year declined when elk numbers were high and increased when elk numbers declined (Caughley and Sinclair 1994; Mills 2007; Murphy and Ruth 2010; Murphy et al. 2011). Hence cougar predation rates on elk were *inversely density-dependent* and explained 49 percent of the variation in the numbers of elk on the Greater Yellowstone Northern Range (fig. 8.2a) [1]. If the elk population had remained near numbers similar to

those during the PW period, the modest increase in cougar kill rates—as related to displacements by wolves and bears and increased predation on adult elk—and modest increases in cougars were unlikely to result in substantially greater offtake of elk by cougars. In this scenario total predation rates of cougars were not related to elk numbers, and cougar predation alone was unlikely to have significantly limited the growth of the elk population in the absence of other factors [2].

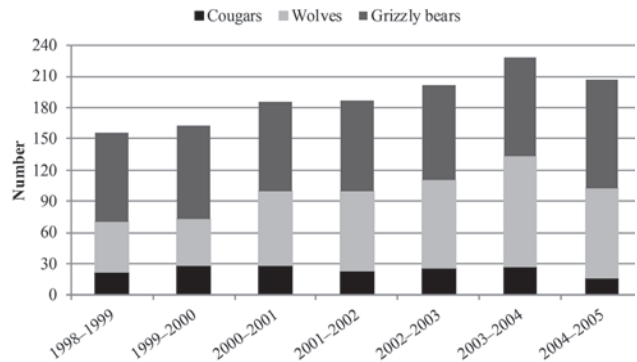
After wolves were freed from soft-release pens, their numbers increased from 21 to 106 through 2003, declined in 2004, and recovered to 108 in 2007—a growth of approximately 13 percent annually between 1995 and 2007 (Hamlin et al. 2009a; Smith and Bangs 2009). As wolf restoration progressed, wolves outnumbered DW cougars by 2:1 averaged over the first two years of our study and by roughly 4.5:1 during the last two years of our study. Wolf predation on cow elk was very similar to that of cougars and varied between less than 2 percent and slightly less than 5 percent of the offtake each year (fig. 8.1). Between the years 1998–99 and 2000–2001, wolves removed less than 5 percent of bull elk and less than 10 percent of elk calves. By 2001–2002,



**FIGURE 8.2.** Total predation rate on elk (see text) of cougars (a) and cougars and wolves combined (b) over the pre-wolf phase and during wolf restoration studies on the Greater Yellowstone Northern Range, 1988–2004. The change in slope from a best fit of a linear relationship to a logistic relationship supports the additive nature of cougar and wolf predation when ignoring other sources of mortality that contribute to lower elk numbers.

offtake of elk calves by wolves jumped to between 23 percent and 34 percent, and offtake of bulls jumped to 13 percent to 21 percent. In combination, total predation rates of cougars and wolves were *more strongly inversely density-dependent* than cougar predation alone and explained 74 percent of the variation in the numbers of elk on the Greater Yellowstone Northern Range (fig. 8.2b) [3].

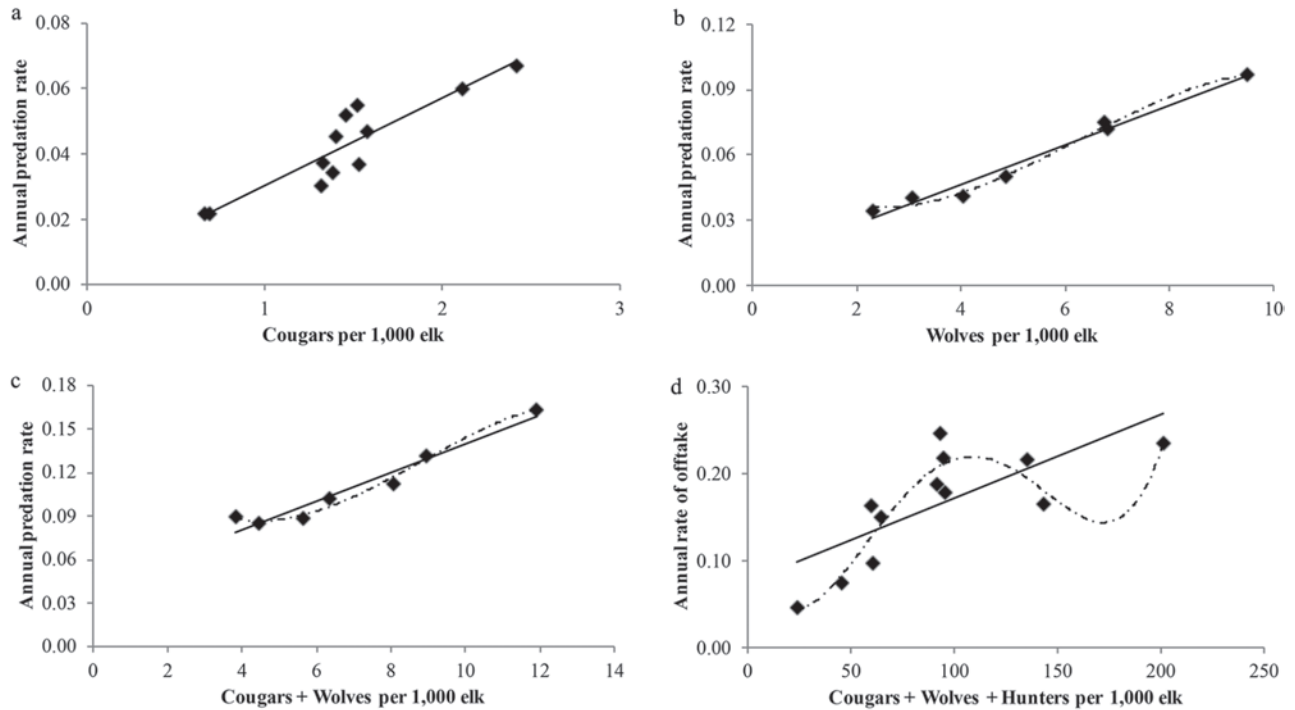
Like wolves, grizzly bears made a remarkable recovery in the Greater Yellowstone Ecosystem, from an estimated 136 in 1974 to a minimum estimate of 405 in 2006 (Craighead et al. 1974; Schwartz et al. 2006b; Hamlin et al. 2009a, 2009b). Therefore, coincident with the increasing wolf population, numbers of grizzly bears also increased on the Greater Yellowstone Northern Range—growing from an estimated 86 in 1998–1999 to roughly 105 at the end of our study. Combined, wolves and bears outnumbered cougars by an average of 8:1 between 2001 and 2004–2005. After wolf restoration, cause-specific mortality estimates of offtake of calves by multiple carnivores increased—grizzly bears accounted



**FIGURE 8.3.** Minimum estimated number of adult, subadult, and kitten cougars and estimated numbers of all age classes of wolves and grizzly bears present on the Greater Yellowstone Northern Range, 1998–2004. Large carnivore numbers ranged from roughly 156 in 1998–99 to a peak of 228 in 2003–4.

for at least 57 percent of elk calf deaths, wolves at least 13 percent, coyotes around 9 percent, and cougars 3 percent of elk calf deaths caused by predators (Barber-Meyer et al. 2008). Mortality of radio-collared Northern Range elk calves during birth through October averaged twice as high from 2003 through 2005 as during the PW years 1987 through 1990 (Barber-Meyer et al. 2008; Hamlin et al. 2009a). The increase in summer mortality appeared to be related to an increase in mortality caused by both species of bears, but it also reflected predation on calves within their first month to month and a half of life.

During wolf restoration, the total estimated numbers of large carnivores ranged from roughly 156 in 1998–1999 to a peak of 228 in 2003–2004 (fig. 8.3). Cougars, wolves, and bears were present at levels consistently above 50 carnivores per 1,000 calves, and the ratio had more than doubled at the point when calf recruitment dropped to 12 to 14 calves in 2001–2002 through the remainder of our study (table 8.1). As wolf and grizzly bear numbers increased along with sustained harvest by hunters, the ratio of calves per 100 cows declined, and the total predation rate of cougars increased as a function of cougars per 1,000 elk (fig. 8.4a) [4]. The annual predation rate of wolves also increased as a function of an increasing ratio of wolves per 1,000 elk, which explained at least 97 percent of the variation in the total predation rate of wolves (fig. 8.4b). Therefore, cougar and wolf predation rates combined increased as the ratio of cougars and wolves to elk increased (fig. 8.4c) [5].



**FIGURE 8.4.** Total predation rate (proportion of prey killed) of cougars (a), wolves (b), cougars plus wolves (c), and annual offtake of cougars, wolves, and hunters (d) as a function of numbers of carnivores and hunters per 1,000 elk. Dashed lines represent polynomial smoothing functions for reference, as a small sample size restricted fitting other than a linear function (solid line, statistics in text). A 3rd order polynomial is shown in (b) and (c), yielding  $R^2 = 0.993$  and  $0.986$ , respectively, and a 4th order polynomial is shown in (d), yielding  $R^2 = 0.859$ .

In a management-directed effort to reduce the elk population, the Montana Department of Fish, Wildlife and Parks implemented a late-season hunt from 1997 through 2004, during which a median 1,100 females were killed (Hamlin et al. 2009b). This translated to hunters removing 3 percent to 10 percent of mainly prime-age cow elk, averaging six years old, until antlerless permits were reduced (Eberhardt et al. 2007). Most prime-age females were harvested during the late-season antlerless hunt, when cows were pregnant, and thus offspring of these females were lost as well (Wright et al. 2006). Although prime-age cows were intentionally reduced through hunter tags and cougars contributed to greater removal of this age group, the survival rates of northern Yellowstone cow elk were not appreciably different between the PW and DW study periods: 83 percent to 84 percent PW and ranging from 76 percent to 81 percent DW (see Hamlin et al. 2009a: 559, table 25.3; Hamlin et al. 2009b).

When we added hunters to cougar and wolf numbers per 1,000 elk, the ratio explained 47 percent to 86 percent of the

variation in annual offtake of elk (fig. 8.4d) [6]. As wolf restoration began (1998 through 2000–2001), hunters, cougars, and wolves combined removed 8–11 percent of bulls, 8–15 percent of cows, and 34–42 percent of calves. During that time hunters removed two to three times as many cows as cougars killed and almost as many bulls as the offtake by cougars and wolves combined, while cougars and wolves took three to ten times more calves than did hunters. In the following years, when wolves were considered colonized or restored—2002 through 2004–2005—the Montana Department of Fish, Wildlife and Parks reached its elk management objectives. The department then reduced the number of tags available to hunters, after which the ratio of hunters per 1,000 elk declined from 131:1,000 in 1998–1999 to 51.5:1,000 by 2004–2005. Although hunter harvest was reduced, the proportion of cows removed annually was sustained at 4–7 percent until the hunting season of 2004–2005 (fig. 8.1). Thus hunters and carnivores combined sustained removal of cows at 9–12 percent; and cougars, wolves, and



hunters removed an equal proportion of cow elk during this time. The percentage of bulls removed jumped to roughly 30 percent, with carnivores—primarily wolves—removing two to four times the number of bulls that hunters took. The percentage of calves removed also doubled, jumping to 60–89 percent, with carnivores responsible for removing nine to fifteen times the number of calves that hunters took.

### Reproductive Value and Nutritional Condition of Elk

Although cougars are classified as opportunistic hunters that more typically select prey at random (Emmons 1987), we found that, like wolves, they did not attack “risky” prey at random, as the potential of injury and death was high. Prime reproductive-age females remained most abundant in the Northern Range elk population, yet neither cougars nor wolves selected prime-age cow elk. Adult elk of high reproductive value were increasingly killed by cougars, and bull elk were increasingly killed by wolves, but only when availability of elk calves declined, causing both carnivores to make adjustments in their diet. Although some of these adults were in poor condition during late winter, in concert with low recruitment, some mortality was likely additive to hunting in affecting elk population growth. Because body condition and pregnancy rates of cow elk declined rapidly beyond 14 years of age, losses of cows greater than 14 years old had a lower impact on population growth than did losses of cows ages 1–14 (Cook et al. 2004).

A proportion of losses in the elk calf component reflected non-additive mortality because calves did not breed during their first year of life and had low reproductive value (Murphy 1998). During their assessment of calf mortality, Barber-Meyer and colleagues (2008) proposed that at least 28 percent and as much as 87 percent of the total mortality caused by predation might have compensated for death that would otherwise have resulted from starvation, accidents, or disease. Using less quantitative methods, other biologists have also suggested that 30 percent to 50 percent of cougar predation is compensatory (Hornocker 1970; Logan and Sweanor 2001). Our rates fell within these ranges—23 percent to 30 percent of calves and adults removed by cougars and wolves during winter were malnourished (femur fat <41 percent) and unlikely to have survived. Another 36 percent to 47 percent were in relatively poor condition (femur fat 41–85 percent), suggesting that they were more vulnerable

to predation than their healthier counterparts; thus many of these losses were compensatory.

Winter severity in the current and previous winter, as well as summer range conditions, have long-term underlying effects on ungulate vital rates and population growth (White et al. 2009a; Hurley et al. 2011; Pierce et al. 2012). Following a severe winter in 1996–1997, the extended drought that began around 2000 and persisted through the duration of our study resulted in the *ecological carrying capacity* of the Northern Range shifting toward one that could support fewer elk, in turn affecting the compensatory-additive continuum of elk mortality (Kie et al. 2003; Murphy and Ruth 2010; Murphy et al. 2011). Hence predation should have become more compensatory as drought continued. Yet comparisons of body fat levels of northern Yellowstone elk in midwinter—February through March—revealed that the condition of elk remained relatively similar in the PW and DW studies (P. J. White et al. 2011). Following wolf restoration, mean midwinter body fat levels of northern Yellowstone elk were among the highest measured in nineteen herds across the western United States, and weights of calves harvested after wolf restoration were at or above those recorded before wolf restoration (Hamlin et al. 2009a; Cook et al. 2010; P. J. White et al. 2011). This corresponded with pregnancy rates of female elk during wolf restoration that were equal to or higher than PW elk pregnancy rates (Hamlin et al. 2009a, 2009b; P. J. White et al. 2011). In combination, these data lend support to the idea that low recruitment of calves during wolf presence was a function of low calf survival, low cow survival, or both (Hamlin et al. 2009a, 2009b; P. J. White et al. 2011).

Outside the winter period, cougars killed elk, mostly calves, in relatively good condition based on femur marrow fat. Yet the compensatory mortality of elk calves may have been compounded by the sustained drought and reduced carrying capacity of the Northern Range. Many young produced at high population densities relative to carrying capacity are born to mothers with few body reserves; consequently, neonates exhibit low body mass and are more likely predisposed to mortality from a variety of sources, including predation (Kie et al. 2003). Further, summer nutrition may be as important to elk and deer population growth as winter nutrition or more so, as energy expenditure in winter relies on nutrition and fat stored during summer (Cook et al. 2004; Tollefson et al. 2010).

The compensatory nature of predation may also depend on the different hunting methods of carnivores, with one carnivore out-competing others by reducing the availability of vulnerable animals for another (Barber-Meyer et al. 2008). Because cougars selected for elk calves to a greater degree than did wolves, they may more commonly kill healthy calves, but this may also come about because wolves, coyotes, and bears beat cougars to the “table” of unhealthy calves. Bears searched for hiding calves and fawns so soon after the birth of these young ungulates and to such an extent that bear predation may have precluded compensatory predation by cougars and wolves until calf condition declined during winter (Barber-Meyer et al. 2008). Adverse spring foraging conditions for elk and for bears during drought years potentially influenced exploitation competition for elk calves and for spring carrion provided by cougars and wolves. And interference competition and loss of carcasses meant cougars killed again more quickly.

### Competition for Live Prey and Carcasses

Cougars sat at the bottom of the dominance hierarchy within the guild of large carnivores—grizzly bears dominated and wolves were second in line (Ruth et al. 2003; Ruth 2004a). This hierarchy was most evident during direct interactions at kills but may not apply as strongly to exploitation competition for prey. Although they did not drive changes in the system, cougars were superior exploitative competitors for elk calves relative to wolves. Because wolves were superior exploitative competitors for adult elk, they should have been able to out-compete cougars as the abundance of calves declined. Increased preference for adult elk by cougars translated to greater risks, including increased detection of large kills by competitors, resulting in: (1) loss of biomass and the subsequent need to kill more frequently, (2) potential for injury or death while killing large ungulates, and (3) potential for injury or death while feeding at and defending a kill. While cougars were generally adept at avoiding direct interactions with competitors, limited prey resources might also result in increased intraspecific competition for food and in starvation, with the latter found in two study areas where cougars competed with wolves and bears subsequent to declines in prey (Ruth 2004a; Kortello et al. 2007). Scavenging and revisitation of old kills by wolves can also increase as elk abundance declines (Becker et al. 2009b). If competition for carcasses increases as a result of declines in

elk, not only may cougars be displaced more frequently from their kills, but they, too, may take greater risks to scavenge from and revisit kills of conspecifics as well as competitors.

On the Greater Yellowstone Northern Range, the loss of meat to scavengers cannot be discounted when estimating total predation rates and limits to prey population growth by carnivores. Cougars are more efficient hunters of small ungulate prey than are wolves (i.e., high success rates; Hornocker 1970) and have lower energy expenditures during consumption of prey than do wolves. However, we propose that in conjunction with landscape characteristics that enhance detection of large prey kills, cougars are less efficient consumers of larger prey in systems with multiple dominant competitors because of their solitary feeding behavior and lower ability to defend kills from scavengers and competitors. Therefore, cougars should and did kill less frequently than wolves, but the biomass they killed approached or exceeded that of wolves because they killed an increasing number of large prey and lost those prey to competitors. These characteristics may lend themselves to cougar predation being found as the stronger predation pressure relative to that of other carnivores in suppressing recruitment of young during prey declines, thus lengthening the time over which a prey population might increase (Pierce et al. 2012).

### BOTTOM-UP TO TOP-DOWN INFLUENCES IN THE SYSTEM

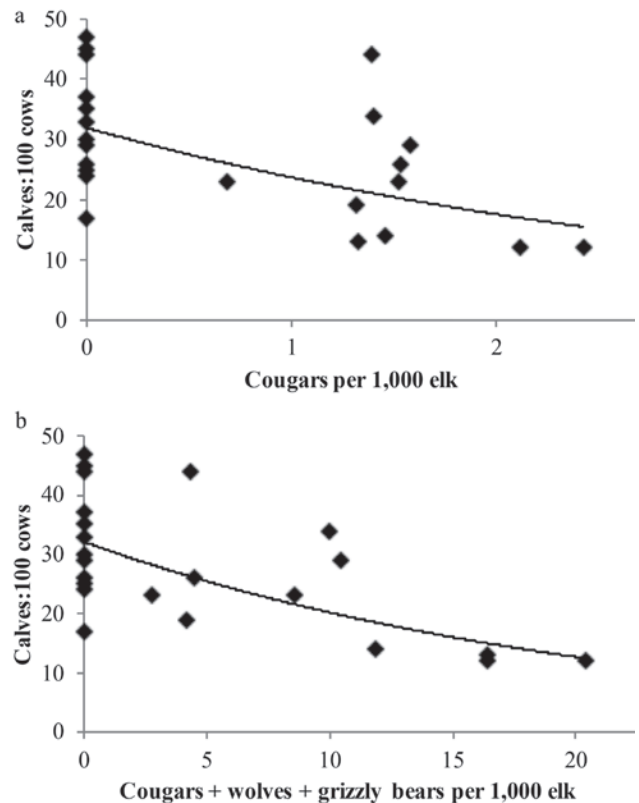
In the period before wolves arrived, the primary causes of mortality for adult elk were hunter harvest and winter kill; predation by cougars, coyotes, and grizzly bears was minimal, with no detectable limitation on growth of the elk population—which continued to grow after the 1988 fires—or of the mule deer population (Singer et al. 1989; Gese and Grothe 1995; Murphy 1998; Knight et al. 1999). Instead of predation, density-dependent intraspecific competition for food by elk, interacting with climate, operated to limit and regulate the Greater Yellowstone Northern Range elk herd as it was near carrying capacity (Houston 1982; Merrill and Boyce 1991; Coughenour and Singer 1996a, 1996b; Singer et al. 1997). Also prior to wolves, the dynamics of an elk population subjected to no human hunting or significant predation in the Madison Headwaters of Yellowstone National Park were found to be *bottom-up regulated* as a result of resource limitation prior to wolves arriving in the system (Garrott et al. 2009a). Between 1991 and 1998, star-

vation during winter was the overwhelming cause of death, accounting for 93 percent of all documented mortalities of radio-collared cow elk and 75 percent of radio-collared calves in the Madison Headwaters of Yellowstone (Garrott et al. 2009b: 508).

Elk populations tend to become limited by predators when high ratios of predators to elk are reached—manifesting primarily through direct impacts on elk calf survival and recruitment—and this has typically occurred when multiple predator species are numerous within the range of one elk population (Hamlin et al. 2009a, 2009b). In combination with hunters removing cows of high reproductive value on the Greater Yellowstone Northern Range, wolves and bears preying heavily on calves, and possibly drought—which initiated the decline in elk by affecting their survival and recruitment—cougar predation added to these other sources of mortality and limited recruitment of calves into the elk population. The combination of these factors led to stronger top-down influences during our DW study.

The lower success of prey capture by wolves, their high energy expenditure during long chases, and social interactions during feeding and territorial defense translated to wolves eating more than would be expected for their body mass. Following restoration into a prey-abundant system, the frequency at which wolves killed prey limited the elk to a greater degree than did cougars in the early years of restoration, but cougars more strongly limited recruitment once other factors initiated a decline in elk (see also Miquelle et al. 2005). During wolf presence the recruitment of elk calves, as indexed by ratios of calves per 100 cows observed in late winter or spring, decreased linearly as the numbers of cougars per 1,000 elk increased—but this occurred as a result of declining elk numbers and increased numbers of total carnivores per 1,000 elk (fig. 8.5a, 8.5b). Calf replacement of cows fell short by an average of 22 to 30 calves per 100 cows, and losses to predation contributed to low recruitment (Hamlin et al. 2009b).

Homogeneous habitats may enable competitive advantages of one carnivore over another. In contrast, heterogeneous landscapes, which provide competition refuges, may enable coexistence of multiple carnivores at levels that support stronger top-down influences than do more homogeneous habitats. A gradient of environmental vulnerability for elk among the complex mosaics of coniferous forest and rugged terrain interspersed with large grassland valleys and pla-



**FIGURE 8.5.** Recruitment rate (calves:100 cows) of elk on the Greater Yellowstone Northern Range relative to numbers of cougars per 1,000 elk (a) and cougars, wolves, and grizzly bears per 1,000 elk (b). Calves:100 cows aligned on the 0 x-axis is data for the years 1968 through 1979 and assumes that predation by cougars and grizzly bears is minimal or nonexistent.

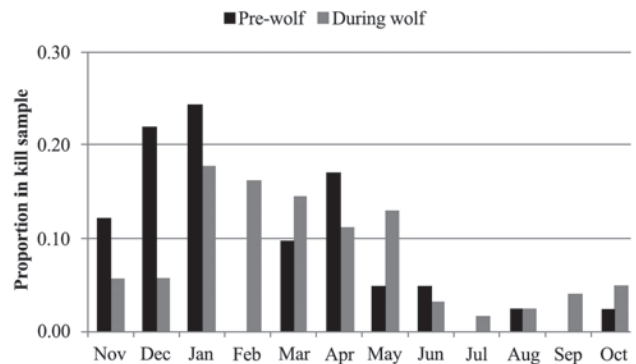
teaus was apparent across the Northern Range. The Lamar River Valley and the Buffalo and Blacktail Deer Plateaus were areas where elk were vulnerable to wolf predation. Yet Northern Range elk continued to use these habitats in spite of low to moderate levels of wolf presence and instead exhibited behaviors that favored detection of predators, such as grouping (Fortin et al. 2005; Mao et al. 2005; Bergman et al. 2006; Kauffman et al. 2007; White et al. 2009c). Fewer elk appeared to roam through steep, topographically complex areas such as those adjacent to the Black Canyon of the Yellowstone. Yet if they foraged in smaller, more dispersed groups within timbered, rocky habitats, their vulnerability to cougar predation potentially increased. We observed elk traveling in single file along narrow trails to access grassy slopes interspersed within the steep, topographically com-

plex habitat, and cougars successfully made kills along and near these trails.

Like mule deer that migrated outside the park, a portion of Yellowstone elk migrated to low-elevation grasslands in the Gardiner area and Paradise Valley. These elk may also have escaped predation by cougars, wolves, and bears, as the carnivores occurred at lower densities as a result of human hunting and conflicts with people that led to management removal actions (Evans et al. 2006; Barber-Meyer et al. 2008). However, those elk that occupied areas outside the park during winter were subject to hunting mortality during our study, which reduced survival rates and altered the age structure of the elk population (Evans et al. 2006). Consequently, hunters and carnivores selected elk from subsets of the population with different age structures and synergistically affected all sex-age classes. Although predation added to hunter removal of prime-age cows and bulls, cougar and wolf predation on adult elk remained concentrated primarily in winter and early spring months (fig. 8.6). Winter and early spring reflected a time when vulnerability of adult elk increased, greater snow depth potentially hampered escape, and migratory travel by elk along trails through cougar habitat presented opportunities for cougars to capture adult elk on forested, steep slopes. Given this combination, where prey migrate from protected to hunted landscapes and are subject to predation in one area and hunter mortality in another, impacts should be more substantial than in areas where prey and carnivores are hunted (as numbers of both are reduced) or in areas where they are both fully insulated and protected from human removals (Evans et al. 2006; Eberhardt et al. 2007).

### COUGARS IN A CHANGING PREDATOR-PREY SYSTEM

Our findings contribute to a growing body of knowledge, yet the time and length of our study influenced the inferences we were able to make from the resulting data. Because our study was of longer duration than many, at fourteen years, and included a pre-wolf understanding of cougar predation, we were able to quantify the manner in which cougar predation added to other sources of mortality. Following the end of our study, increased intra- and interspecific competition could have reduced cougar growth and production further. But did drought and reduced summer range conditions have a greater long-term underlying effect on ungulate vital rates and population growth? Did declining elk and addi-



**FIGURE 8.6.** Monthly distribution of all adult female elk in the cougar kill sample prior to ( $n = 47$ ) and during wolf restoration ( $n = 124$ ) on the Greater Yellowstone Northern Range, 1987–2005. Few adult females were killed during non-winter months.

tive predation result in cougars switching to alternative prey after the end of our study? Did intraspecific competition for prey and space result in cougars turning on cougars, or did interspecific competition increase with more cougars killed by wolves? If so, does this relax predation pressure and slow the decline of elk or deer populations? This kind of interwoven intraguild predation—where carnivores are engaged in a mixture of competition and predation—may have far-reaching effects on how natural communities function, yet may take decades to understand more fully (Polis et al. 1989; Polis and Holt 1992; Holt and Polis 1997; Linnell and Strand 2000; Creel et al. 2001).

As was apparent from the years preceding wolf restoration, predation and hunting do not always fully compete with each other, but sometimes they do. Following the successful restoration of wolves to an area supporting an already diverse suite of large carnivores and in conjunction with hunter harvest of antlerless elk, we saw a slow decline in the elk herd toward the state of Montana's population objective for elk near the end of our study. In the years following completion of our study, elk continued to decline; and calf production, although improving somewhat at 24 and 19 calves per 100 cows in 2006 and 2007, respectively, was still less than the 31 calves per 100 cows in the years preceding 2001 (Cross et al. 2009). With the population objective for elk achieved and the continued decline in elk, the number of permits issued for the antlerless Gardiner late elk hunt was reduced from 1,102 in 2005 to just 100 permits during the 2006–10 seasons, and the late-season hunt was eliminated altogether in 2011.



By 2011 the size of the Northern Range elk herd had experienced a reported 70 percent drop from the 16,791 elk counted in 1995 (Hamlin et al. 2009a, 2009b).

Reducing late-season hunter harvest, as occurred near the end of our study, perhaps provides one of the quickest, although not necessarily most accepted, management strategies for ungulate populations that include migratory herds moving between non-protected areas and protected areas where predation plays out naturally. Fewer prime-age adults removed by hunters should require fewer surviving calves to replace them, but such effects are likely to differ for smaller ungulate species where adults are more equitably killed by carnivores because of their size. Yet even if hunting pressure remains low or is decreased further on the Greater Yellowstone Northern Range, low numbers of elk might persist until drought abates or predator to prey ratios decline (Hamlin et al. 2009a).

In prey declines, carnivore populations often naturally lag behind those of prey (Logan and Sweaner 2001). Considering that food resources were not a limiting factor during our study, selection for abundant and vulnerable prey species by both cougars and wolves fits predictions of carnivore prey selection and resulted in high dietary overlap indicative of exploitation competition (MacArthur and Pianka 1966; Sunquist and Sunquist 1989). Where multiple large carnivores are present—and competition is expected to increase as resources become limiting—the decline may be hastened for subordinate cougars, with lower body condition, reduced survival, and reduced recruitment becoming apparent (Schaller 1972; Brand et al. 1976; Mech 1977b; Knick 1990; Mowat et al. 1996; Ruth 2004a). One example comes from a small elk population of approximately 600 wintering in Banff National Park, Canada, where the ratio of carnivores (excluding bears) to elk was 0.5 wolves per 100 elk in 1999. Following two years of human management conducted by relocating approximately 26 percent of the elk in 1999 to 2000 and another approximately 8 percent the following year, the elk population continued to decline, and cougar and wolf numbers peaked at 10 cougars and wolves per 100 total elk in 2001. During that time the cougar diet switched to less abundant deer and bighorn sheep. Cougar numbers quickly declined to almost half, with food limitation and one death from wolves as contributing factors. By the end of the study in 2003, when elk numbers were around 150 to 200, there were roughly 7.4 cougars

and wolves per 100 elk (as calculated by us using data from Kortello et al. 2007).

With increasing numbers of bears and wolves on the Greater Yellowstone Northern Range at the closing stages of our study, exploitation competition for calves apparently persisted. Yet several years after our study ended, biologists suspected that carnivore numbers were responding to the decline in the elk population—wolf numbers dropped from 94 in 2007 to 37 in 2010, and grizzly bear numbers also decreased. Increased intraspecific aggression and disease affected numbers of wolves (Smith and Bangs 2009). In turn, the reduction in the number of wolves and the elimination of the late-season hunt were expected to result in some increase in the elk population. Reductions in prey suggest that cougar numbers may also have declined, while reductions in competitors could have proved beneficial for the big cats. And as long as hunting habitat is sufficient, cougars appear capable of making a living where prey are few because forested, rough landscapes enable cougars to hunt successfully (fig. 8.7), as we discuss further in subsequent chapters. This raises the question of to what densities prey decline before they become limiting for cougars in multi-carnivore and multi-prey systems. And what is the response or lag time before starvation, intraspecific competition, or other factors reduce cougar numbers as a consequence of limited prey? There are now several studies documenting the impact of intraguild competition among large carnivores, but examples of one large carnivore driving another to localized extinction are rare (Creel et al. 2001; Miquelle et al. 2005).

## SUMMARY

During a sixteen-year time span, cougars did not drive changes in the system in the absence of other factors. In the years preceding wolf restoration, cougars removed less than 2 percent of adult elk and 9–17 percent of calf elk. Predation by cougars, coyotes, and grizzly bears remained minimal, with no detectable limitation on growth of the elk population—which continued to grow after the 1988 fires. Accumulated information from multiple co-occurring studies reveals the transition of the Greater Yellowstone Northern Range elk population from one that was regulated bottom-up by food limitation to a population that is more strongly limited top-down by multiple predators. Following the arrival of wolves, cougars removed less than 5 percent of cow elk, but their predation on calves jumped from 10



**FIGURE 8.7.** *Where hunting and escape habitat is sufficient, cougars appear capable of making a living where prey are few because forested, rough landscapes enable them to hunt successfully and to conceal kills from scavengers and competitors. Photo by Tony Knuchel, Hornocker Wildlife Institute/Wildlife Conservation Society.*

percent in the early wolf restoration years to 20–60 percent as calves became less available after wolves were fully colonized. Assessment of the proportion of the elk population killed annually by cougars revealed an inversely density-dependent, or depensatory, relationship. When the total predation rates of cougars and wolves were added together, the depensatory relationship increased because both predators acquired a larger proportion of the elk population. As elk declined, cougars were superior exploitative competitors of elk calves compared to wolves, while wolves were superior at exploiting adult elk—although the majority of adults were in poor health. On the Greater Yellowstone Northern Range, cougars, wolves, and bears reached numbers between 156 to 228, and their predation limited recruitment of elk calves, particularly when their ratio consistently exceeded 50 carnivores per 1,000 elk calves. The number of calves available was then insufficient to replace losses of prime-age cow elk, which were removed primarily by hunt-

ers, ultimately achieving the Montana Department of Fish, Wildlife and Parks management goal of reducing Northern Range elk numbers outside the park.

The combined effects of multiple carnivores and migration of a proportion of elk to areas where hunting was sustained through the end of our study combined to influence all sex and age classes of elk. Since the end of our study, cougar predation potentially continued to contribute to strong limitation of recruitment of elk calves and perhaps increased predation on prime-age cow elk. Alternatively, if cougars increasingly competed with wolves and with other cougars for food, their numbers may have declined, thus relaxing their contribution to limiting the elk population. With our study ending prior to elk becoming a limiting resource, such lingering questions reveal that even with the return of wolves to a landscape of abundance and their rapid increase in numbers, the response of other species and restructuring of the ecosystem has taken well over ten years.

### **PART 3**

#### **Landscape Use**

##### *Do Cougars Avoid Wolves?*

Without resources, organisms will die, and so the contest to find, harvest, transport, store and retain possession of resources is an essential part of the struggle for survival.

PAUL KEDDY, *COMPETITION* (2001: 1)







## CHAPTER 9

### How Might Cougars Respond to Wolves?

The fitness of an individual cougar or wolf depends on its acquisition of food and mates, maintenance of home ranges or territories, interactions with other carnivores to defend food resources, and avoiding direct interactions that could be lethal (Murphy et al. 1999; Crooks 2002; Mech and Boitani 2003b; Dickson et al. 2005). Daily, seasonally, and annually, a combination of forces affects behaviors, with spatial dynamics driven not only by an individual's basic needs and experience but also by environmental conditions and landscape structure (Murphy et al. 1999). Habitat use and spatial arrangement of individuals are two of the more important aspects of species' niches to consider, as it may be less energetically costly for a subordinate individual to shift away from a dominant competitor or use different habitat features in a landscape than it is to change diet or periods of activity (Schoener 1974). Both cougars and wolves are able to live under a range of conditions, which in turn might enable or lead to diverse spacing behaviors and habitat use in areas where they occur sympatrically. In this chapter we provide specific predictions on how cougars might alter their use of the landscape in response to wolves.

When we consider how two or more carnivores may orient spatially within an area, there are some general patterns. Carnivores of differing size may specialize on different prey types or sizes of prey, and in such cases of low dietary overlap, the two species often overlap spatially but may or may not use different habitats (Rosenzweig 1966; Johnson et al. 1996). In assemblages where two carnivores are more closely matched in size or one is dominant over the other, exploitative competition for food may be more likely, and habitat partitioning is more common. A diversity and abundance of prey might allow cougars and wolves to exploit similar food without resulting in partitioning of habitat, but this

might change as food becomes limited and more difficult to acquire. In the event that types and abundance of food become more limited, exploitation competition should intensify, and as a result the subordinate carnivore would be expected to occupy adjacent areas that offer more marginal habitat or food (Koehler and Hornocker 1991; Litvaitis 1992; Johnson et al. 1996; Durant 1998). Yet the degree of habitat homogeneity or heterogeneity across a landscape and fluctuations in the environment, perhaps seasonally, influence whether organisms exploit resources in such a way as to promote their coexistence or detract from it (Chesson 1985; Keddy 2001; Holdo and Roach 2012).

In homogeneous habitats use of diverse habitats may be limited, and space may therefore be used more similarly by prey and for hunting by carnivores, perhaps resulting in increased direct interactions (Kunkel et al. 1999; Creel and Creel 2002). Alternatively, heterogeneous habitats—such as those including a mix of large meadow systems, forested areas, and topographically complex terrain—provide a mosaic of habitat features enabling subordinate individuals to avoid rivals that are clumped in distribution, potentially reducing competitive encounters and enhancing coexistence (Shorrocks 1991; Durant 1998). Making use of these *competition refuges*, where competition is reduced, can be crucial for the persistence of species with low competitive ability (Sih 1987; White et al. 1994; Durant 1998; Denno et al. 2005). This outcome has occurred for San Joaquin kit foxes avoiding coyotes and for cheetahs avoiding African lions and hyenas (Durant 1998; Nelson et al. 2007).

## HYPOTHESES AND PREDICTIONS

Before undertaking the data collection phase of this research, we gathered information from other studies on spatial-

habitat use and interactions between large carnivores. We then developed a set of questions and predictions about how we expected cougars might respond as wolves became reestablished on the Greater Yellowstone Northern Range. As our study progressed and we understood cougar population and predation characteristics better from the PW study, additional hypotheses and predictions arose.

Given the potential outcomes just mentioned, our working hypothesis was that wolves, as dominant carnivores, would limit the distribution of cougars across a range of spatial scales through interference and exploitation competition. If wolves monopolize areas of high prey density, then spatial avoidance by cougars might reduce competition for prey in certain habitats as well as reduce direct interactions with wolves. Hence, to reduce or avoid exploitation and interference competition, cougars should seek out different habitats, spatially avoid wolves, and perhaps alter their activity patterns (Ruth 2004a; Kortello 2005). As a result, cougar spatial or habitat use—or both—of the Northern Range ecosystem should differ from the spatial distribution and habitat use of cougars prior to wolf restoration. If cougars adequately avoided wolves by making such adjustments and using competition refuges, they might successfully partition resources with wolves. In addition, coexistence of the two should also be possible if cougars were superior to wolves at exploiting certain resources (Polis et al. 1989). For example, researchers in South America suggested that because cougars took a greater range of prey sizes, they were superior exploitative competitors to jaguars, which placed them at greater advantage when faced with human-induced prey and habitat changes (Nuñez et al. 2000; Maxit 2001).

Although we expected that the spatial distribution and habitat use of cougars during wolf restoration should differ from their distribution and habitat use prior to wolf restoration, there were several alternative hypotheses to explore when considering how cougars might respond to wolf presence. For example, cougars might make spatial adjustments to avoid wolves, yet use the same habitat types and food resources, thus maintaining their fundamental niche in the ecosystem. Alternatively, how DW cougars orient home ranges and their overall spatial distribution might be similar to the situation of PW counterparts, but DW cougars might select habitat components differently than PW cougars. Perhaps DW cougars select similar habitats but show a preference for certain components, such as remaining in or near

escape cover, and thus the magnitude of selection might increase over that of their PW counterparts. In table 9.1 we outline and provide rationales for alternative hypotheses of cougar habitat and space use during wolf restoration relative to habitat and spatial use of cougars prior to wolves. In table 11.1 we provide specific predictions relative to the environmental variables or characteristics used when we modeled the habitat preferences of cougars and wolves.

### HOME RANGE SIZE, FIDELITY, AND OVERLAP

The size and orientation of home ranges are among the most basic of the ecological parameters regularly described for a given species and are important for understanding population characteristics and habitat use as well as for establishment of protected areas and management boundaries (Schwartz 1999; Woodroffe and Ginsberg 2000; Kernohan et al. 2001). Home range size, home range fidelity, and the orientation of home ranges to neighboring cougars and to wolf territories all provide insight into whether spatial changes occurred as cougars adjusted to the presence of wolves (White and Garrott 1990).

Defending a large territory poses several problems for both cougars and wolves. For wolves, defending a territory must be energetically efficient, and defense must not take so much time or energy as to hamper courtship, copulation, and care of young (Wilson 1975; Mech and Boitani 2003a). This is also true for male cougars as they defend home ranges from conspecifics and make large movements that must be energetically efficient yet allow time for courtship and mating with females (Hornocker 1970; Logan and Sweanor 2001, 2010). Female cougars maintain a home range primarily for rearing and protection of offspring but also make movements, sometimes beyond the boundaries of their maternal home range, to announce their presence to males when they are ready for breeding.

As wolf restoration progressed, we anticipated that prey would be spatially and temporally less predictable, the spatial structure of cougars would be less well established and predictable, and cougar movements would be more dynamic as they moved to areas that provided security and refuge from competition and encounters with wolves (Mao et al. 2005; Gower et al. 2009b).

Considering these potential outcomes, we made the following predictions regarding metrics of home range size, fidelity, and overlap, which we address in chapter 10. These

**TABLE 9.1.** Hypotheses and reasoning associated with cougar habitat and space use during wolf restoration relative to habitat and space use prior to wolves (PW) on the Greater Yellowstone Northern Range.

| <i>Hypotheses</i>       | <i>Reasoning</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
|-------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 1. Habitat =, space =   | <ul style="list-style-type: none"> <li>• Cougars have not reached carrying capacity demographically or environmentally.</li> <li>• Cougars never abandon their basic niche because population pressure is not sufficient to change the collective use of habitat, despite the fact that food resources have declined and wolf pressure is high.</li> <li>• New resident females fill in available spaces, but they still use the environment the same way as long-established females.</li> <li>• Males may shift their individual territories, but their use of the environment does not change.</li> <li>• Effects of wolves are not (yet) sufficient to cause a change in the use of space or the environment.</li> </ul>                                                                                                 |
| 2. Habitat =, space >PW | <ul style="list-style-type: none"> <li>• Cougars could have the same habitat use as before because they do not change their fundamental niche and they shift into similar environments.</li> <li>• Cougars expanding into new areas to avoid wolves and new areas could be either (1) composed of same quality habitat or (2) composed of suboptimal habitat that is still used in the same way.</li> </ul>                                                                                                                                                                                                                                                                                                                                                                                                                  |
| 3. Habitat =, space <PW | <ul style="list-style-type: none"> <li>• Cougars could have the same habitat use as before because they do not change their fundamental niche and they shift into similar environments.</li> <li>• Existence of a new competitor precludes use of some areas and could cause a retraction in the collective use of the study area and a shift in the location of individual ranges.</li> <li>• Prey space use is limited, or a reduction in prey could cause a retraction in the collective use of the study area and a shift in the location of individual ranges.</li> </ul>                                                                                                                                                                                                                                               |
| 4. Habitat ≠, space =   | <ul style="list-style-type: none"> <li>• Habitat use might change significantly because cougars are collectively facing constraints that alter habitat use: prey are reduced, prey habitat use has altered, and new competitor forces result in selection for increased security.</li> <li>• Analysis of habitat use for individual cougars (particularly new ones) reveals differences in how they use the environment.</li> <li>• Structural changes to the habitat have forced different patterns of use.</li> <li>• Well-established females are still spatially stable, new females are spatially stable once they settle in. Males may shift. However, changes in habitat use need not be accompanied by a change in the use of space if escape terrain from wolves is available within cougar home ranges.</li> </ul> |
| 5. Habitat ≠, space >PW | <ul style="list-style-type: none"> <li>• Cougars expand into new areas, but those areas are either composed of different habitat or the population faces constraints that alter use of the habitat, such as prey distribution and habitat use have changed or a new competitor forces cougars to select habitat that provides increased security.</li> <li>• Structural changes to the environment could have precluded use of certain habitats.</li> </ul>                                                                                                                                                                                                                                                                                                                                                                  |
| 6. Habitat ≠, space <PW | <ul style="list-style-type: none"> <li>• Consistent with the hypothesis of a strong wolf effect: cougars retract from wolf habitats (i.e., reduce their collective use of the study area), shift their territories related to wolf pressure or changes in prey distribution, or both. Habitat use changes because cougars are also forced to use the environment differently, regardless of where their new ranges are.</li> <li>• Structural changes to the environment could have precluded use of certain habitats.</li> </ul>                                                                                                                                                                                                                                                                                            |

predictions are also summarized in the final synthesis chapter (chapter 17, table 17.2), showing which predictions were supported.

1. Prior to wolf presence, we hypothesized that home range sizes would be large and that fidelity to a particular site or home range would be high, as established cougars predictably used the same sites for access to mates, foraging, and security. As wolves were restored in the study area and cougars adjusted to increasing wolf densities, home ranges of cougars should fluctuate in size to a greater degree than prior to wolf presence. In avoiding wolves, cougars might shrink home range sizes to fit into areas between wolf territories. Alternatively, their home ranges might increase while

balancing the need to seek out prey yet avoid wolves, thus making larger movements to incorporate disjunct patches of habitat within the mosaic of habitat on the Greater Yellowstone Northern Range.

2. If cougars responded to increased wolf density and use across the Northern Range, we predicted that home range sizes would be more dynamic than prior to wolves. We also predicted that site fidelity would be lower, as cougar movements should reflect shifts toward areas that provide refuge from competition. We expected PW cougars to exhibit an established and stable social structure of conspecifics, resulting in greater fidelity of PW males and females relative to fidelity of DW males and female cougars as they adjusted to increasing numbers and distribution of wolves. In either

study phase we expected that established female cougars would exhibit strong fidelity to home ranges relative to males because familiarity with prey and escape resources in an area should enhance the survival of offspring (Logan and Sweanor 2001).

3. Because they maintain and defend more exclusive chunks of the landscape, territories of male cougars typically overlap much less with conspecifics than female cougar home ranges overlap with those of other females (Logan and Sweanor 2001; Mech and Boitani 2003b). In avoiding wolves, cougars—particularly females—should overlap the most secure or optimal habitat to a greater degree than prior to wolves, thus sharing resources to a greater extent. Consequently, overlap between cougars should be greater during than prior to wolf restoration. Therefore, regardless of study phase, female-female overlap should be higher than male-male overlap. The large territories of adult males, which enable access to multiple females and which males actively defend, suggest that males should overlap females more than they overlap other males (more F-F than M-M pairs; Logan and Sweanor 2001).
4. We expected that cougar home ranges and wolf territories should overlap extensively. However, both carnivores use parts of their home range, a core area, more intensively than the rest of the home range or territory. The likelihood of direct encounters in these more peripheral areas is probably rather low, since these areas of overlap are used much less than core areas (Creel and Creel 2002). As a result, we expected that the areas used most intensively would provide the best evidence as to whether cougars were able to segregate themselves spatially from wolves. Accordingly, core areas of cougars should be situated away from or in between core areas of wolf territories. Hence, we predicted that there would be less overlap of cougar and wolf core areas than of their full home ranges. During winter, when elk are concentrated on winter ranges and cougars are less likely to be able to segregate themselves spatially from wolves compared to summer, overlap of cougar home ranges and core areas with wolves should be greater (Kunkel et al. 1999; Ruth 2004a).
5. Cougars tend to be crepuscular and nocturnal hunters and are likely to be located in bed sites within secure habitats during daytime (Seidensticker et al. 1973; Ackerman 1982; Beier et al. 1995; Dickson et al. 2005). As both cougars and wolves relied primarily on elk, which are strongly active during dawn and dusk, we predicted that activity

patterns of the two carnivores should be similar, with peaks in activity corresponding to crepuscular and nocturnal periods (Eberhardt et al. 1984; Kufeld et al. 1988; Green and Bear 1990; Beier et al. 1995; Ager et al. 2003). Differences in activity would support predictions that cougars and wolves avoided one another. Cougar activity substantially different from that predicted based on peaks in primary prey activity would support cougars adjusting their activity to avoid wolves, at the cost of hunting at times when prey are less active. However, research on a variety of predators has demonstrated that substantial differences in activity times do not result in low dietary overlap (Litvaitis 1992). Therefore, temporal segregation is not an effective means of resource partitioning unless different activity periods result in access to different prey.

6. Cougars may adjust behaviors depending on the magnitude of risk as well as distance to and availability of secure habitat. Accelerated movements in areas of high risk might signify flight behavior, particularly if movements are greater than in areas with low risk of encounter (Arundel et al. 2007). When traveling in the periphery of their home range, particularly when they are roaming within the core area of wolves where risk of encounter should be greatest, we expected cougars to travel more rapidly than when they moved within their own core area.

To assess cougar spatial structure further before and during wolf restoration, we were also interested in assessing several predictions relative to two underlying hypotheses about cougar social organization, given our set of conditions and increasing wolf density. A first hypothesis, put forth by Hornocker (1969, 1970) and Seidensticker and colleagues (1973) during their studies in the Idaho wilderness, postulated that the social organization of cougars was determined by an intrinsic territoriality, or *land tenure system*, that acted to limit numbers of cougars and to maintain population stability. Hornocker and Negri (2010: 238) later clarified that “all species seek to maximize reproduction, but they must first be established in a situation favorable to reproductive effort such that home ranges are established first around food and shelter and that reproductive opportunity is provided for as a consequence of first having food and shelter.” Once established, males in particular require a certain amount of space regardless of the food supply. Second, while studying mostly female cougars in California, Pierce and co-workers



(2000b) evaluated the land tenure hypothesis and proposed that cougar social structure was most strongly determined by abundance and distribution of food resources—a prey-abundance influence. Whereas home range size of female cougars is thought to be tied to prey availability, male home ranges are tied to a second factor as well: the availability of females, with breeding opportunities set by the number of females' home ranges a male's home range overlaps (Trivers 1972; Sandell 1989; Ross and Jalkotzy 1992; Murphy 1998). Logan and Sweanor (2001) later clarified with the two-strategies hypothesis: female cougars are food or prey limited, and males are limited by the size of the territory they can defend to maximize the number of breeding females regardless of prey abundance and distribution.

These hypotheses led us to consider several predictions by first assuming the absence of interspecific competitors, where cougar home range sizes should reflect the spatial distribution of forage resources and access to mating opportunities (Sandell 1989; Murphy et al. 1999; Logan and Sweanor 2001; Maletzke 2010). Assuming that prey resources remained constant but the number of cougars changed, some predictions were as follows:

1. Under the land tenure hypothesis, as the number of conspecifics increases, home range sizes of males and females and overlap should decrease and fidelity to home ranges should increase.
2. Under the prey-influence hypothesis, as the density of cougars increases or decreases, home range size, overlap, and fidelity for both males and females should remain unchanged.
3. The two-strategies hypothesis predicts that female home range size, overlap, and fidelity should remain constant. Home range size of males should be influenced more by the abundance and distribution of females than of prey, with male home range size decreasing with increasing densities of females more than with increasing densities of males, while home range size should increase following removal of conspecifics (Logan and Sweanor 2001, 2010).

If prey abundance changes but cougar density is held constant, then:

1. Under the land tenure hypothesis, home range sizes and overlap should remain constant as elk density declined between the PW and DW periods.

2. The two-strategies hypothesis suggests that female home range size should increase and overlap and fidelity should decrease (increased competition and searching) as prey decline. Under this scenario, female home range size would be most influenced by prey, with home ranges sizes expanding as prey availability declined in the during wolf period. Logan and Sweanor (2001) also hypothesized that if prey availability declined without a corresponding increase in female home range size, then females were exhibiting a degree of avoidance of one another. If females were avoiding one another, we should then see a decrease in overlap between females as their density increased. Under the two-strategies hypothesis there should also be no change in male home ranges or overlap as food changes, but these should change as females become less predictable spatially.
3. If prey density most strongly influenced the size of male home ranges, we would expect to see an increase in home range size as elk abundance decreased between the PW and DW periods, even if the number of mates and competitors was increasing. Further, in our study area, male home range size and overlap should be greater in the pre-wolf period because of lower intraspecific competition with other males compared to later, as the male population increased and became established during wolf restoration.

## SPATIAL-HABITAT USE

A central prediction of competition theory is that animals will alter their use of habitat under the risk of competition (Caughley and Sinclair 1994). In particular, when the dominant competitor is a better interference competitor or better able to exploit patches of habitat that provide food and security, density of the dominant competitor may reach such a level that the subordinate competitor reduces the risk of encounters by avoiding the dominant competitor directly or by partitioning available resources (Creel et al. 2001). Avoidance by a subordinate species might involve occupying different habitats, hunting at different times, or switching to a different prey resource to minimize risk and perhaps provide an advantage over its competitor, enabling coexistence of multiple species (Schoener 1974; Seidensticker 1976; Bothma et al. 1984; Durant 1998; Fedriana et al. 1999; Karanth and Sunquist 2000).

Demonstrating exploitation competition requires documenting that one species negatively affected resource use by

another species (Petren and Case 1996). Yet documenting that cougars alter their resource use because of interference and exploitation competition with wolves has not been adequately investigated, primarily because no other study has had the opportunity to evaluate resource use prior to and during wolf restoration. Considering our hypotheses and that cougars are subordinate, we made the following predictions, which we address in chapter 11. These predictions are again summarized in the final synthesis chapter (chapter 17, table 17.2), showing which predictions were supported.

1. Cougars should seek out and use habitats where wolves are at low density, thus avoiding areas of high wolf use.
2. In the heterogeneous habitat of the study area, cougars should be better exploiters of steep, rocky terrain and forested habitats that provide both hunting and escape cover. Hence cougars during wolf presence should show increased preference, reflected as increased magnitude, for habitats that provide escape and hunting cover. Because females support offspring for 60 percent to 80 percent of their reproductive life, they should select forested and rugged terrain and more strongly avoid wolves than would male cougars. Wolves should dominate and select for lower slopes and elevations and more open grassland and shrubland habitats than do cougars.
3. As dominant competitors, wolves might monopolize areas of high prey density and competitively exclude cougars. In avoiding wolves, cougars would then be displaced from the best foraging habitats and would be found in areas with lower densities of prey compared to their competitors (Lima and Dill 1990; Durant 1998; Creel et al. 2001).
4. Avoidance should increase as the density and overlap with wolves increases from summer into winter. Alternatively,

the ability of cougars to avoid wolves may be greater during summer, when competitor density is lower as a result of greater dispersion and less overlap (Durant 1998). Because prey move to higher elevations and space is not limited, cougars should also move to higher elevations and should be able to separate spatially from wolves more than during winter.

5. The overall distribution of cougars should be different between PW and DW reestablishment time frames. Given a growing cougar population (Murphy 1998), cougars should first fill in the best habitats that provide access to food, cover, and mates. Subsequently, as the population grows toward carrying capacity within optimal habitat, new immigrants should be relegated to more marginal habitats at the periphery of the most suitable areas, with a resulting increase in overall spatial extent. If, however, the population was constrained by wolf presence, cougars should increase their use of the best habitat in the core of their range, potentially resulting in an increased density within habitats that provide for security. Such habitat shifts might result in reduced foraging opportunities (Lima and Dill 1990).

In chapters 10 and 11, we test the ideas set forth in our hypotheses and predictions (summarized in table 9.1) to address how cougars moved and used the landscape as they responded to wolves. In the final chapter of part 3, we synthesize the information and examine whether, as a response to wolves, cougars sought out competition refuges that resulted in portioning of resources between the two species. We also examine our findings in relation to other studies to obtain a clearer understanding of competition between large carnivores.

## CHAPTER 10

### Spatial Responses of Cougars to Wolf Presence

The area a cougar or wolf pack occupies during a specified time encompasses distinct properties—food, security, mates—required to meet the individual's biological needs to survive and reproduce (Burt 1943; White and Garrott 1990). Being mostly solitary, cougars establish and traverse large independent home ranges (Logan and Sweanor 2010; Fecske et al. 2011). Adult female cougars typically use non-defended home ranges that overlap widely among individuals, with average sizes ranging from 73 to 685 km<sup>2</sup>. Adult males mark their home ranges with scrapes and urination behaviors, defending their territories against other adult males, and home ranges may be as large as 826 km<sup>2</sup> (Logan and Sweanor 2010; Fecske et al. 2011). Wolf packs generally occupy exclusive territories, which also vary widely in size among geographic areas—from 10 to 1,645 km<sup>2</sup> (see Fuller et al. 2003, table 6.3, 172–74).

In this chapter we present data on home range and territory sizes of cougars and wolves and then test whether home range sizes were related to cougar density, prey availability, or the density of wolves. We estimate fidelity of cougars to home ranges over time, overlap of home ranges, and daily movements within home ranges to assess changes between PW and DW periods. We use these analyses as an initial step to test predictions set forth in chapter 9 regarding how cougars and wolves sort out the landscape.

#### DETERMINING HOME RANGE SIZES

We used the *fixed kernel*, a non-parametric method for estimating an animal's home range with a utilization distribution (UD; appendix C; Worton 1989; Kie et al. 1996). We defined the *home range* as the area encompassing 95 percent of the cumulative UD. In reality, cougars spent more time near the center of their range than in the periphery. As a result, we

delineated two areas of use within the home range. We defined the area of most intense use, or *core area*, as encompassing 50 percent of the UD and the periphery, or area of less intense use, as encompassing 51 percent to 95 percent of the UD.

We compared the fixed kernel, adaptive kernel, exponential power, bivariate circle, and bivariate normal methods of estimating a home range using the program Animal Space Use V1.1 (Horne and Garton 2006a, 2007). We chose the fixed kernel method based on goodness-of-fit simulations on a sample of 53 female and 12 male home range years. We describe the smoothing parameter chosen, *cvc-h*, in appendix C (see Horne and Garton 2006b). We calculated 95 percent and 50 percent volume contours and home range sizes with the Home Range Extension for ArcView® (Rodgers and Carr 1998).

We obtained 3,484 Very High Frequency (VHF) locations from repeated sampling of 24 radio-collared adult cougars (15 female, 9 male) during the PW study and 3,249 VHF locations of 24 radio-collared adult cougars (16 female, 8 male) as wolves were restored in the study area. In addition, we obtained 14,435 Global Positioning System (GPS) locations on 10 adults in the DW study. To ensure that successive locations were spatially independent and that reliable comparisons between individuals and study phases were made, we calculated cougar home ranges by first combining kill site locations with weekly flight and ground locations restricted to daytime, 0800 to 1800 hours, and then limiting this set to locations three days apart. This sampling period was considered biologically independent because: (1) cougars are localized at kill sites for an average of three–four days and move between kill sites for three–four days (Murphy 1998; Ruth 2004a), (2) cougars are capable of traversing their home range in a single day, and (3) previous studies have used a

similar time span for biological independence of locations in calculating home ranges (see Murphy 1998; Logan and Sweanor 2001).

We used the location data described to generate home range estimates for 14 PW adult cougars (10 females, 4 males) and 16 DW adult cougars (12 females, 4 males; table 10.1). Annual home ranges were calculated for adult cougars that were present on the study area each year for an average of three years (range = 2 to 6 years) for PW adults and an average of four years (range = 2 to 7 years) for DW adults. Using area-observation curves, we found that a minimum of 30 locations were required for a stable home range estimate, similar to the number of locations in other studies (Gese et al. 1990; Logan and Sweanor 2001; Frey and Conover 2007; Kortello et al. 2007). We estimated 44 and 42 annual home ranges for which we had an adequate number of locations in the PW and DW restoration study periods, respectively.

Although some cougars moved between summer and winter ranges while others did not, we did not estimate home ranges on a seasonal basis because of a small sample size of biologically independent locations per individual. Thus our annual estimates incorporated both winter and summer movements from November of one year through October of the subsequent year. Because we expected that as wolves were restored their density could influence cougar home range size, we further tested whether home ranges and core areas of cougars differed between early and late wolf colonization, but we found no differences [1]. Because cougars used similar-size areas during early and late wolf restoration, we pooled all cat ranges and compared PW to DW data.

Repeated locations on wolves by Wolf Project personnel yielded 10,719 locations on three to eight packs between 1998 and 2005 (D. Smith, National Park Service, unpubl. data). Wolves easily traversed their territories in a single day and typically spent less than a day at each kill; hence we limited wolf data to 1 location per pack per day to ensure independence of locations, resulting in an average of 58 (range = 30 to 97) locations per pack per year (see discussion). We used these data to generate 44 home ranges for a total of eleven packs monitored over an average of four years (range = 1 to 8 years) per pack.

### HOME RANGE SIZES OF COUGARS AND WOLVES

As wolves were restored and increased in number, female cougars maintained home range and core area sizes similar

to those of females in the PW study [2]. Prior to wolf restoration, female cougars occupied home ranges averaging 242.0 km<sup>2</sup> in size, and their home ranges were about 40 percent the size of the average area of 609.0 km<sup>2</sup> used by males (table 10.1, fig. 10.1a, 10.1b) [3]. Average core areas of PW females were similarly smaller, at 50.6 km<sup>2</sup>, about 37 percent the size of the 136.5 km<sup>2</sup> average core area used by PW males [4]. During wolf restoration, female home ranges averaged 258.5 km<sup>2</sup> and core areas averaged 57.2 km<sup>2</sup> (table 10.1, fig. 10.1c). Females' home ranges and core areas remained significantly smaller than males' average home ranges of 343.9 km<sup>2</sup> and core areas of 78.8 km<sup>2</sup> (table 10.1, fig. 10.1d;  $\alpha = 0.10$ ) [5].

Despite these similarities, DW female home ranges and core areas were about 75 percent the size of male home ranges, compared to the 40 percent documented for PW females. The change toward female and male home ranges becoming more similar in size after wolf restoration resulted from a 42 percent to 44 percent reduction in the average sizes of DW male home ranges and core areas compared to those of PW adult males [6].

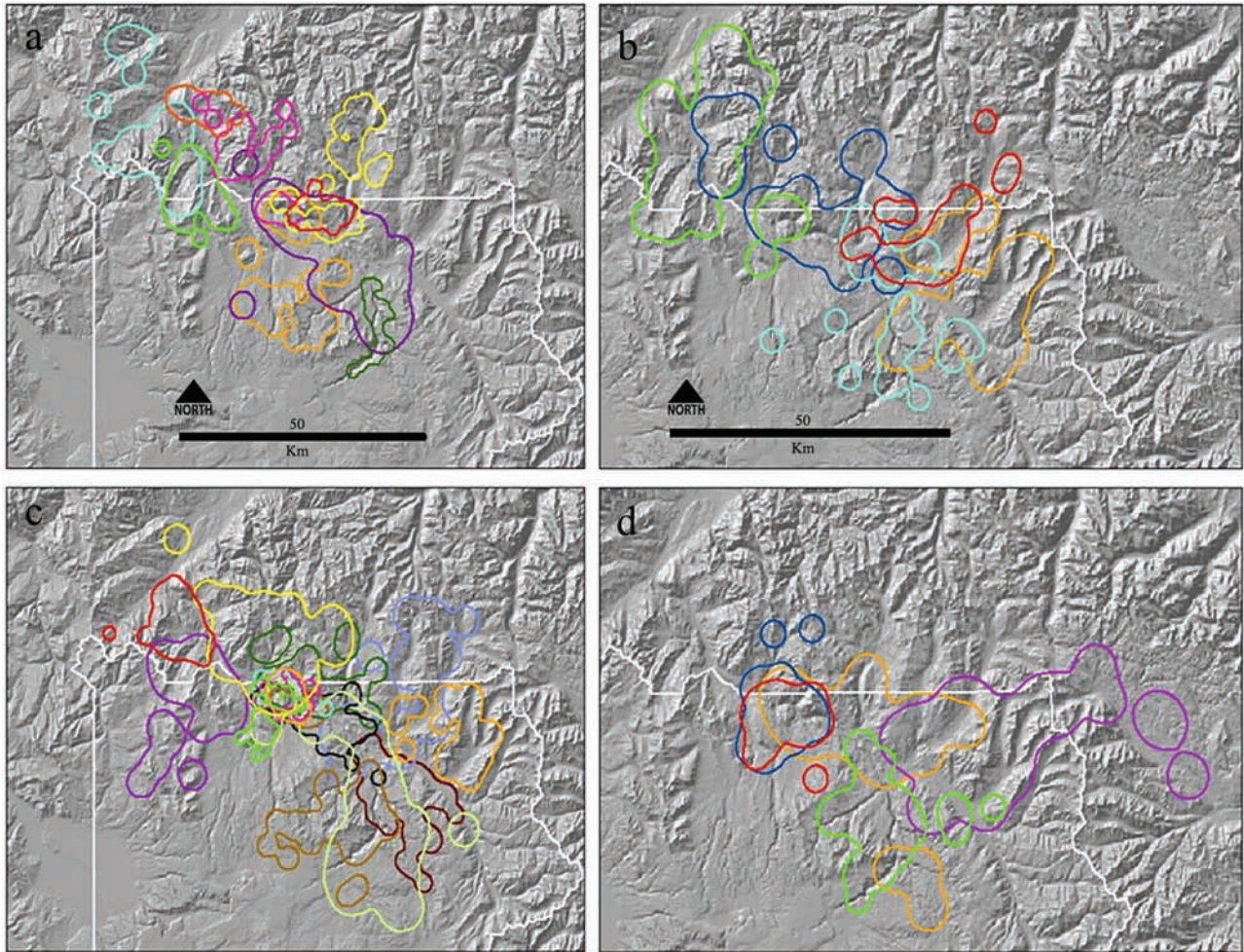
Although female home ranges, on average, were smaller than those of males, several females in both study periods maintained annual areas that rivaled those of males. For instance, females 35 and 53 in the PW study and females 47, the same female 53, and female 120 in the DW period maintained annual home ranges averaging roughly 400 to 500 km<sup>2</sup>—a result of their moving between separate summer and winter areas as they followed migrating prey. These larger home ranges probably also reflect the more fragmented patches of forested, rugged terrain adjacent to broad, open valleys of the central and eastern portions of the Greater Yellowstone Northern Range, which cougars moved between when hunting (fig. 10.2). The western third of the study area, along the Black Canyon of the Yellowstone, contained relatively contiguous forested and rugged cover at lower elevations and received less snow (fig. 10.3). Consequently, females (and thus males) that resided in this area probably maintained smaller home ranges because prey were accessible year-round and the area provided more contiguous stalking and escape cover.

Annual territory and core area size averaging 380.1 km<sup>2</sup> and 72.5 km<sup>2</sup>, respectively, for eleven wolf packs on Yellowstone's Northern Range differed from annual home range sizes and core areas of cougars in the PW and DW study phases (table 10.2; fig. 10.4) [7]. Larger-bodied or pack-forming animals



**TABLE 10.1.** Annual core area and home range size for fourteen adult cougars prior to wolf restoration and sixteen adult cougars during wolf restoration, Greater Yellowstone Northern Range, 1987–2005. SD = standard deviation; core areas are 50 percent fixed kernel; home ranges are 95 percent fixed kernel.

| Study Phase and Gender | Cougar ID        | No. Years | No. Locations/<br>Year | Fixed Kernel Estimate (km <sup>2</sup> ) |      |       |       |
|------------------------|------------------|-----------|------------------------|------------------------------------------|------|-------|-------|
|                        |                  |           |                        | 50%                                      | SD   | 95%   | SD    |
| PRE-WOLF               |                  |           |                        |                                          |      |       |       |
| Females                | F5               | 5         | 46                     | 58.0                                     | 13.4 | 310.5 | 44.5  |
|                        | F9               | 5         | 41                     | 44.5                                     | 25.7 | 205.9 | 130.2 |
|                        | F16              | 4         | 46                     | 37.2                                     | 19.7 | 152.1 | 72.1  |
|                        | F17              | 2         | 50                     | 65.2                                     | 16.8 | 268.5 | 60.7  |
|                        | F30              | 3         | 51                     | 51.0                                     | 9.0  | 197.7 | 25.3  |
|                        | F32              | 4         | 41                     | 40.6                                     | 29.2 | 177.8 | 124.4 |
|                        | F34              | 2         | 51                     | 17.5                                     | 9.0  | 76.5  | 35.3  |
|                        | F35              | 2         | 45                     | 90.0                                     | 23.1 | 548.2 | 198.2 |
|                        | F49              | 3         | 42                     | 37.7                                     | 16.6 | 210.7 | 79.8  |
|                        | F53              | 2         | 66                     | 113.3                                    | 29.8 | 505.2 | 149.3 |
|                        | across all years |           |                        | 50.6                                     | 27.9 | 242.0 | 148.2 |
| Males                  | M8               | 6         | 42                     | 136.8                                    | 55.2 | 581.1 | 239.7 |
|                        | M28              | 3         | 44                     | 162.9                                    | 54.9 | 742.4 | 284.1 |
|                        | M29              | 4         | 49                     | 134.3                                    | 83.9 | 663.3 | 471.0 |
|                        | M51              | 3         | 39                     | 112.3                                    | 33.5 | 458.8 | 129.2 |
|                        | across all years |           |                        | 136.5                                    | 56.9 | 609.0 | 292.7 |
| DURING WOLF            |                  |           |                        |                                          |      |       |       |
| Females                | F47              | 7         | 38                     | 97.9                                     | 41.8 | 426.6 | 177.8 |
|                        | F53              | 3         | 47                     | 96.0                                     | 39.7 | 407.6 | 152.8 |
|                        | F101             | 5         | 38                     | 38.4                                     | 18.8 | 147.6 | 48.8  |
|                        | F105             | 3         | 37                     | 52.9                                     | 60.0 | 231.2 | 262.1 |
|                        | F106             | 4         | 39                     | 37.0                                     | 18.3 | 155.6 | 78.7  |
|                        | F107             | 6         | 34                     | 80.8                                     | 49.2 | 360.7 | 171.1 |
|                        | F111             | 3         | 40                     | 19.1                                     | 6.3  | 94.6  | 51.0  |
|                        | F112             | 4         | 33                     | 15.2                                     | 5.9  | 75.3  | 22.2  |
|                        | F115             | 4         | 35                     | 53.5                                     | 26.6 | 272.3 | 166.4 |
|                        | F120             | 4         | 53                     | 93.2                                     | 54.3 | 520.7 | 303.7 |
|                        | F123             | 4         | 47                     | 60.3                                     | 19.4 | 318.9 | 83.9  |
|                        | F125             | 5         | 37                     | 37.4                                     | 19.3 | 161.9 | 72.2  |
|                        | across all years |           |                        | 57.2                                     | 41.4 | 258.5 | 182.3 |
| Males                  | M127             | 4         | 39                     | 45.2                                     | 10.2 | 189.5 | 32.7  |
|                        | M131             | 3         | 34                     | 125.0                                    | 62.7 | 559.3 | 384.2 |
|                        | M137             | 2         | 34                     | 62.1                                     | 7.0  | 260.1 | 29.1  |
|                        | M148             | 2         | 35                     | 101.1                                    | 60.0 | 444.3 | 239.4 |
|                        | across all years |           |                        | 78.8                                     | 50.5 | 343.9 | 254.4 |



**FIGURE 10.1.** Home ranges of cougars before and during wolf restoration on the Greater Yellowstone Northern Range, Montana and Wyoming: pre-wolf, nine adult female cougars (a) and five adult males (b); with wolves present, thirteen adult females (c) and five adult males (d). Home range size and orientation from the pre-wolf year November 1990–October 1991 and the during wolf year November 2000–October 2001 are displayed as examples, being the years when the greatest number of resident adults were monitored. Broken polygons reflect the separate summer and winter areas used by some cougars. For comparison between studies, the graphic shows only those individuals originally marked within Yellowstone National Park (white line); annual home ranges are 95 percent fixed kernel.

have greater metabolic needs and thus generally require larger areas than do smaller-bodied or solitary animals (Logan and Sweaner 2001; Mech and Boitani 2003b). Wolves did maintain territories that were 65–68 percent larger, and core areas were 42–51 percent larger than average annual home range sizes and core areas of female cougars in both study phases [8]. But in the prey-rich environment prior to wolves, male cougar home ranges and core areas were 1.7 to 2.0 times larger than average wolf home range and core area

sizes. Wolf territories were 42 percent smaller than those of PW male cougars, and wolf core areas were half the size of the core areas of PW male cougars [9]. In contrast to predictions from body mass and metabolic demands, the smaller home range and core areas traversed by DW male cougars resulted in average cougar home range and core area sizes remarkably similar to those of wolf packs [10]. An exception occurred in the first year after wolves were released from pens, when the Druid pack traversed a territory of 1,500 km<sup>2</sup>, which was





**FIGURE 10.2.** View from petrified trees of Specimen Ridge looking across the broad valley known as Little America, frequented by the Slough Creek and Specimen Ridge wolf packs. Photo by Dan Stahler, Hornocker Wildlife Institute/Wildlife Conservation Society.

two and half times larger than the largest male cougar home range of 614 km<sup>2</sup> for cougar M<sub>148</sub>. When averaged across cougars and wolf packs, Ruth (2004a) similarly found that cougars and wolves maintained annual home ranges and territories of equal size in the North Fork of the Flathead Valley, Montana: fixed kernel home ranges of 270 km<sup>2</sup> for cougars and 230 km<sup>2</sup> for wolf packs and core areas of 35 km<sup>2</sup> and 36 km<sup>2</sup> for cougars and wolves, respectively.

Why should the home range sizes of male cougars during wolf restoration be substantially different from those of PW males while female home ranges did not differ? Comparisons with other studies may lend insight, even though there is wide variation in home range size arising from differences in analytical methods used to calculate home ranges, differences in landscape structure, and intensity of human hunt-

**TABLE 10.2.** Mean annual home range and core area sizes for cougars before and during wolf restoration on the Greater Yellowstone Northern Range, Montana and Wyoming. Pre-wolf = 1987–95; during wolf = 1998–2005; home ranges are 95 percent fixed kernel (FK); core areas are 50 percent fixed kernel.

| Phase and Species  | N  | Mean  | SD    | Median | Minimum | Maximum |
|--------------------|----|-------|-------|--------|---------|---------|
| 95% FK HOME RANGE  |    |       |       |        |         |         |
| Pre-wolf F         | 30 | 229.8 | 133.7 | 209.8  | 51.5    | 688.3   |
| Pre-wolf M         | 14 | 652.7 | 282.4 | 564.9  | 310.3   | 1,356.5 |
| During wolf F      | 30 | 226.1 | 172.9 | 151.9  | 49.0    | 606.7   |
| During wolf M      | 9  | 291.1 | 138.9 | 275.0  | 127.4   | 613.6   |
| Wolves (all packs) | 44 | 380.1 | 261.1 | 314.4  | 29.6    | 1,556.3 |
| 50% FK CORE        |    |       |       |        |         |         |
| Pre-wolf F         | 30 | 47.8  | 23.5  | 45.8   | 11.1    | 106.3   |
| Pre-wolf M         | 14 | 146.4 | 52.9  | 136.7  | 74.0    | 258.5   |
| During wolf F      | 30 | 51.0  | 40.2  | 34.9   | 9.5     | 139.6   |
| During wolf M      | 9  | 69.9  | 34.0  | 58.7   | 29.6    | 143.6   |
| Wolves (all packs) | 44 | 72.5  | 39.9  | 62.1   | 17.9    | 191.6   |

ing (Pierce et al. 1999; Logan and Sweanor 2001; Herfindal et al. 2005; Robinson and DeSimone 2011). After limiting our comparison to other studies where prey were migratory, we noticed that the average annual home range sizes of Greater Yellowstone Northern Range cougars, roughly 250 km<sup>2</sup> for females, were very similar to those in six of nine hunted (199 to 249 km<sup>2</sup>, Maletzke 2010) and non-hunted (246 km<sup>2</sup>, Robinson and DeSimone 2011) populations in northern latitudes where prey migrate (fig. 10.5a). This suggested that female cougars meet metabolic demands for survival and rearing offspring with some consistency across more northern latitudes. Home range sizes of PW male cougars were also similar to those in other studies, including a non-hunted population in Montana (603 km<sup>2</sup>, Robinson and DeSimone 2011) and a heavily hunted population in Washington (753 km<sup>2</sup>, Maletzke 2010). Male home ranges during wolf restoration fell on the lower end of the spectrum (fig. 10.5b). On the one hand, these comparisons suggested that male cougars in the PW study were responding primarily to avoiding other male cougars while also seeking access to females. On the other hand, cougars experienced some level of hunting mortality, which can alter social structure and result in larger home ranges (Maletzke 2010; Robinson and DeSimone



**FIGURE 10.3.** During winter population monitoring and capture work, Toni Ruth listens for signals of radio-collared cougars in core cougar habitat above the Black Canyon of the Yellowstone River. Containing relatively contiguous forested and rugged cover at lower elevations, the western third of the study area received less snow and provided cougars with refuge from competition with wolves. Photo by Erin Shanahan, Hornocker Wildlife Institute.

2011). Before delving further into questions of why male home ranges shrank and female home ranges did not, we need to gain understanding of whether cougars maintained fidelity to home ranges and how much home ranges overlapped with those of other cougars and wolves, addressed in the paragraphs that follow. We then also assess the effect of cougar density and prey abundance on home range size, given the presence of interspecific competitors and in light of social organization hypotheses set forth in chapter 9.

### FIDELITY OF ADULT COUGARS TO HOME RANGES

Cougars may show high fidelity to home ranges from one year to the next, yet over longer time frames, such as two to three years, shifts may be more obvious (Logan and Sweanor 2001). Because core areas were the most intensively used areas, less fidelity to core areas might reveal adjustments to changing conditions that were not apparent when examining home ranges. Thus, in addition to home ranges, we examined fidelity of cougars to their core areas. We calculated fidelity indices for each adult cougar during pairs of years, one ( $FI_1$ ) or two ( $FI_2$ ) years apart, where annual (95 percent) fixed kernel home range and core area (50 percent) estimates were obtained for location sample sizes greater than or equal to 30, as earlier described.

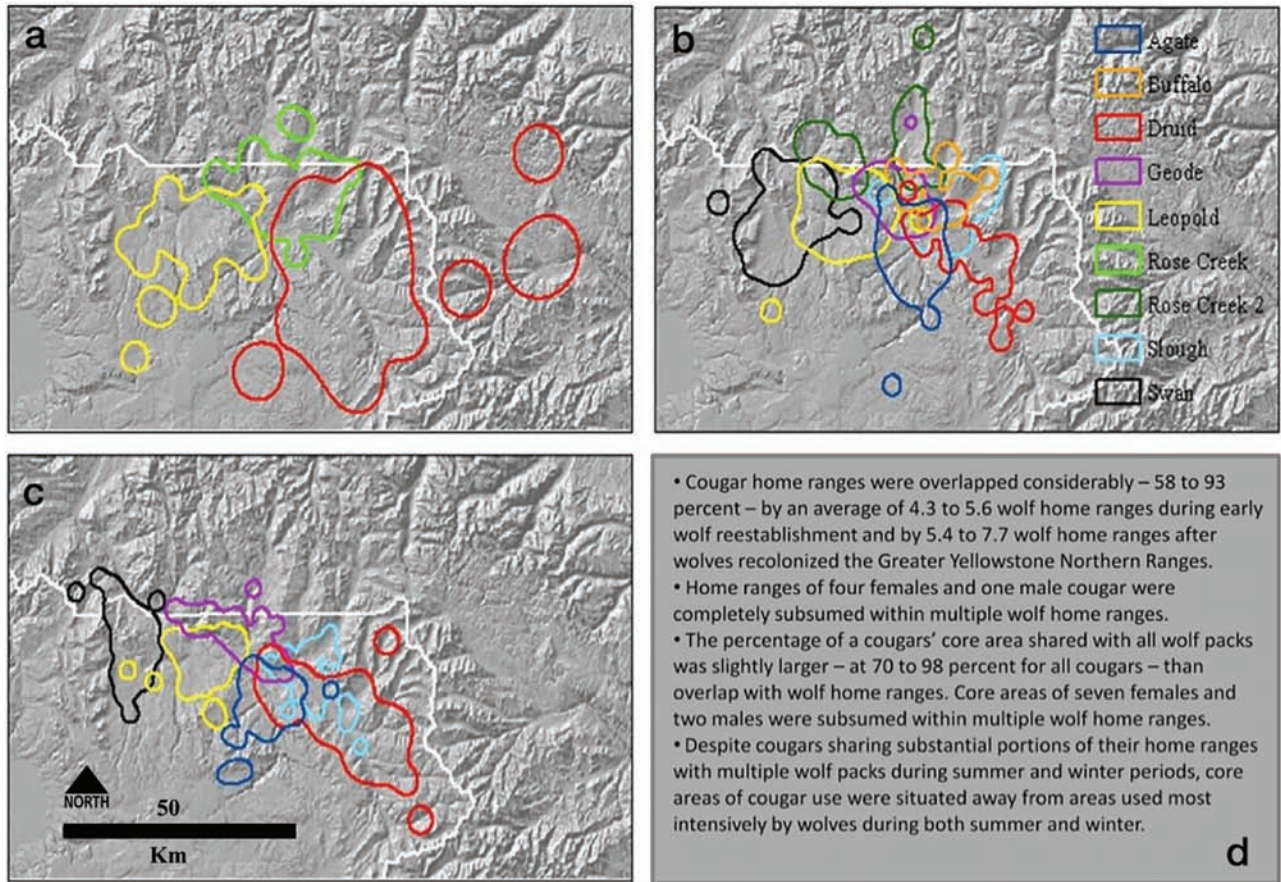
We used Bhattacharyya's affinity (BA; Bhattacharyya 1943) to evaluate whether radio-collared cougars remained in the same approximate area each year [11]. Bhattacharyya's affinity is a function of the product of two utilization distributions (UDs) and equals the joint distribution of the animal's two UD's. In contrast to standard measures of percentage overlap that may indicate high fidelity of an individual to its home range even when the areas of most intense use are not the same, the BA incorporates the intensity of use in each home range (Seidel 1992; Kernohan et al. 2001; Fieberg and Kochanny 2005). The BA index ranges between 0 for two home ranges with no overlap and 1.0 for two home ranges with identical UD's.

Prior to and during wolf restoration, male and female cougars were generally faithful to their annual home ranges from year to year, but their core areas within those home ranges shifted from one year to the next. Female and male cougars tended to remain in one area over the course of two years, reflecting high fidelity to home ranges in both the PW and DW studies. Within three years' time, some shifting of annual home ranges occurred—a finding similar to that reported for cougars in the San Andres Mountains, New Mexico (table 10.3; Logan and Sweanor 2001) [12]. Core areas of cougars shifted more than home ranges did, as reflected by estimates of core fidelity that were substantially lower than those for home range fidelity in both study phases (table 10.3) [13]. Because outer boundaries of home ranges about other cougars and wolves, they may be more rigid than core areas. Plasticity in core areas may reflect variation in how cougars utilize patches of habitat from year to year within the portion of their home range that provides access to food and secure cover while minimizing interaction with other cougars and competitors.

Next we examined whether home ranges and core areas of cougars shifted more during than prior to the presence of wolves. Fidelity from one year to the next and after two years' time,  $FI_1$  and  $FI_2$ , was greater during wolf restoration than prior to wolves at both the 95 percent home range and 50 percent core area (table 10.3, fig. 10.6a, 10.6b) [14]. In other words, cougar home ranges and core areas were more stable after than before wolf restoration, which ran counter to our hypothesis that as cougars avoided wolves, their home range patterns would reflect less overall fidelity to particular sites.

Stability of home ranges over long time periods is advantageous for females because stability enables knowledge



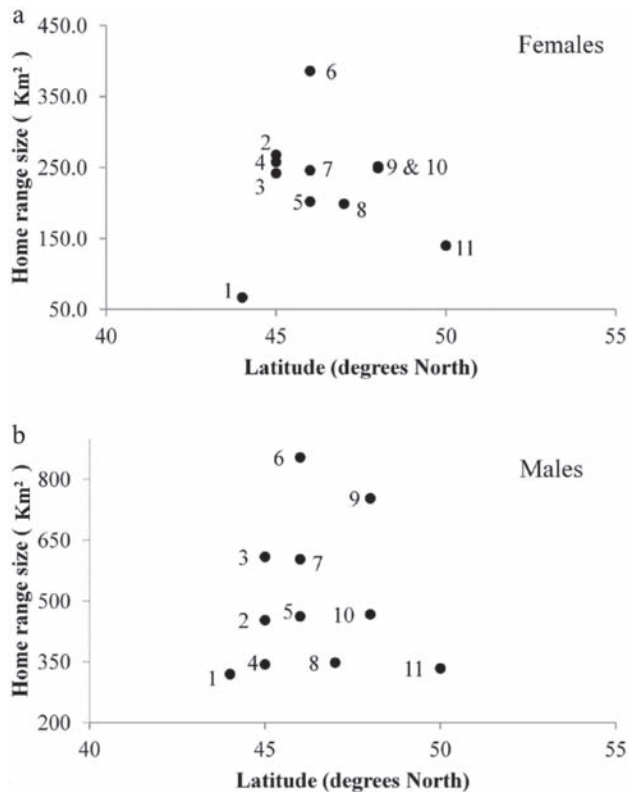


**FIGURE 10.4.** Home ranges of wolf packs displayed as examples of territory size and orientation during early restoration (a, three packs, November 1997–October 1998), peak numbers after colonization (b, eight packs, November 2002–October 2003), and near the end of our study (c, six packs, November 2004–October 2005). Most wolf packs resided on the Northern Range within Yellowstone National Park (white line). Annual home ranges are 95 percent fixed kernel.

about where to seek out prey, the best den sites for giving birth, and the most secure cover for avoiding other cougars and more dominant carnivores. Through social predictability, site fidelity also enables recognition between neighboring females and overlapping resident males, which are less likely than new immigrant males to harm females or their kittens (Logan and Sweanor 2001). Yet at times, female cougars may shift home ranges as a strategy that benefits reproductive success through avoidance of other females, to avoid conditions that pose hazards to a female or her offspring's survival, or to accommodate philopatric daughters (Sunquist 1981; Logan and Sweanor 2001, 2010). While other studies have documented shifts of adjacent resident females into home ranges vacated by other females, complete abandon-

ment of an established home range by female cougars, such as we documented (see text box 10.1), is quite rare (Laing and Lindzey 1991; Maehr et al. 1991; Spreadbury et al. 1996; Maehr 1997b; Logan and Sweanor 2001).

Male cougars should also benefit from long-term fidelity because it enables recognition of and familiarity with potential mates as well as with neighboring males, thus enhancing reproductive opportunities, decreasing potentially aggressive interactions with competing males, and increasing overall fitness (Logan and Sweanor 2001). Shifts by male cougars previously documented in other studies occurred when immigrant adult males arrived within or adjacent to resident male home ranges, when resident females within the male's territory died, and when neighboring adult males died or were experimen-



**FIGURE 10.5.** Annual home range size of cougar females (a) and males (b) in northern latitudes where prey are migratory. MCP = minimum convex polygon; FK = fixed kernel.

- 1 = Bighorn Mountains, WY (MCP, Logan 1983)
- 2 = Big Creek, ID (MCP, Seidensticker et al. 1973)
- 3 = Greater Yellowstone Northern Range prior to wolves (95% FK, Murphy 1998)
- 4 = Greater Yellowstone Northern Range during wolf restoration (95% FK, this study)
- 5 = Fish Creek, MT (MCP, Murphy 1983)
- 6 = Garnet Mountains, MT, heavily hunted (95% FK, Robinson and DeSimone 2011)
- 7 = Garnet Mountains, MT, no hunt (95% FK, Robinson and DeSimone 2011)
- 8 = Cle Elum, WA, lightly hunted (99% FK, Maletzke 2010)
- 9 = Kettle Falls, WA, heavily hunted (99% FK, Maletzke 2010)
- 10 = North Fork of the Flathead River, MT, wolves and moderately hunted (95% FK, Ruth 2004a)
- 11 = Sheep River, Alberta, Canada (MCP, Ross and Jalkotzy 1992)

tally removed (Seidensticker et al. 1973; Logan and Sweanor 2001). Although territories of three males shifted prior to wolf presence, they did not shift more than PW female home ranges when viewed over a three-year period [15]. We did not

**TABLE 10.3.** Fidelity to home ranges and core areas of male and female cougars on the Greater Yellowstone Northern Range, as measured with Bhattacharyya's affinity (BA), before wolves (1987–95) and during wolf restoration (1998–2005). Data are for pairs of years one (FI<sub>1</sub>) and two (FI<sub>2</sub>) years apart; SD = standard deviation; home ranges are 95 percent fixed kernel; core areas are 50 percent fixed kernel.

|                 |          | 95% BA     |           | 50% BA     |            |           |            |
|-----------------|----------|------------|-----------|------------|------------|-----------|------------|
|                 | <i>n</i> | <i>Avg</i> | <i>SD</i> | <i>Med</i> | <i>Avg</i> | <i>SD</i> | <i>Med</i> |
| FI <sub>1</sub> |          |            |           |            |            |           |            |
| Males           |          |            |           |            |            |           |            |
| Pre-wolf        | 11       | 0.45       | 0.18      | 0.57       | 0.33       | 0.20      | 0.39       |
| During wolf     | 8        | 0.51       | 0.15      | 0.54       | 0.42       | 0.10      | 0.44       |
| Females         |          |            |           |            |            |           |            |
| Pre-wolf        | 21       | 0.51       | 0.16      | 0.45       | 0.31       | 0.17      | 0.29       |
| During wolf     | 33       | 0.62       | 0.17      | 0.57       | 0.46       | 0.16      | 0.46       |
| FI <sub>2</sub> |          |            |           |            |            |           |            |
| Males           |          |            |           |            |            |           |            |
| Pre-wolf        | 8        | 0.40       | 0.24      | 0.40       | 0.28       | 0.22      | 0.27       |
| During wolf     | 2        | 0.51       | 0.06      | na         | 0.39       | 0.09      | na         |
| Females         |          |            |           |            |            |           |            |
| Pre-wolf        | 12       | 0.37       | 0.19      | 0.41       | 0.25       | 0.17      | 0.26       |
| During wolf     | 19       | 0.54       | 0.17      | 0.57       | 0.37       | 0.18      | 0.37       |

observe such shifts by resident males until the very end of our wolf restoration study (see text box 10.1).

Given that a high degree of fidelity is consistent with a strong social structure, including familiarity with conspecifics, food, and habitat, our findings of increased stability of home ranges corresponded with the stronger social structure of resident cougars during than prior to wolf restoration (Irwin and Peek 1983; Edge et al. 1986; Linnell and Anderson 1995). As cougars were restored in the study area prior to wolves, new males and females arrived and were less familiar with conspecifics, and females shifted ranges to accommodate daughters. Males likely shifted in response to removals by hunters at the north end of the study area and as they sorted out the landscape to acquire access to females at lower density than during wolf presence.

After wolves were released from restoration pens, cougars may have made adjustments to their presence quickly during the three years preceding our DW study. Those adjustments possibly continued during 1998–99, but we did not have the data to assess fidelity at a finer scale. During wolf restoration, cougars had greater familiarity with conspecifics, as

evidenced by an older age structure and both genders maintaining fidelity of home ranges in prime, secure habitat that enabled avoidance of wolves in the DW study period. This was also evident for core areas—core areas of DW cougars shifted less than those of PW cougars. Although a decline in prey may also eventually stimulate home range shifts or possibly abandonment as cougars seek more productive habitats (Logan and Sweanor 2001), and this trend should have occurred as the availability of prey declined during wolf restoration, we did not observe any shifts or abandonment of home ranges until the end of our study. As we discuss later, although elk declined, they apparently did not become a limiting resource for cougars during our study.

### OVERLAP WITH OTHER COUGARS

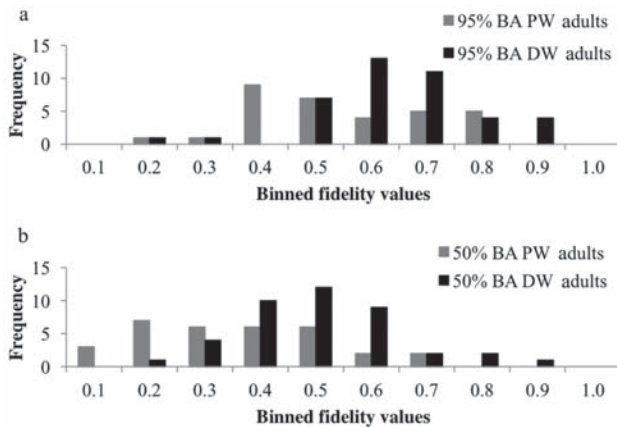
Because the number of cougars increased during the PW period and wolf densities rapidly increased after wolf restoration, we expected variation in overlap of cougars within early and late portions of each study phase, yet we found no difference in percentage overlap of home ranges for female-female and male-female pairings [16]. Thus we pooled all overlap data within the PW period and all data within the DW study when testing for differences in static overlap of home ranges between the PW and DW time periods.

Prior to restoration of wolves, each adult female cougar shared part of her annual home range with 1.0 to 2.4 other

female cougars, while each adult male cougar shared parts of his home range with an average of 2.0 to 3.3 adult females (table 10.4). During wolf presence adult females shared parts of their annual home range with a slightly greater number of other females—2.3 to 3.4 other females, on average (table 10.4). Adult male cougars shared parts of their home ranges with almost double the number of females—4.0 to 5.7—as were observed prior to wolf restoration.

In addition to the number of overlaps, we used two methods to quantify spatial overlap between cougars—percentage total overlap and a utilization distribution overlap index. For comparison to other studies, we calculated total overlap as the percentage of a cougar's home range that was overlapped by all other cougars of the same and opposite sex. We did this by dividing the area of overlap for each animal by that animal's annual home range area. We examined total overlap for the year in which we had the most information—November 1990 to October 1991 in the PW study and November 2000 to October 2001 for the wolf restoration study. To determine the intensity with which overlap areas were used by two cougars, we quantified space-use sharing between cougar pairs using the utilization distribution overlap index (UDOI; Fieberg and Kochanny 2005). If two cougar home ranges did not overlap, a UDOI value of 0 resulted. A UDOI value of 1.0 resulted if two cougar home ranges overlapped completely (100 percent) and the cats used their home ranges uniformly. Yet UDOI could be greater than 1.0 if two cougar home range UD's were non-uniformly distributed and had a high degree of overlap. A UDOI greater than 1.0 was indicative of 100 percent overlap and both animals spending most of their time in a relatively small common area, compared to UDOI equal to 1.0, where the animals shared a larger area more uniformly.

When we assessed overlap within and between study phases, we found that females tended to share a greater percentage of their home range and core area with males than with other females, although the significance of non-parametric tests varied by time period and overlap measure (table 10.5) [17]. Prior to wolves, female home ranges overlapped an average of 50 percent with PW other females and 68 percent with PW males. No female's home range was completely engulfed by other females or males in the PW period. Female cougars during wolf presence shared a slightly larger amount of their home range with other DW females and males—69 and 77 percent, respectively—with three of eleven females sharing greater than 95 percent of



**FIGURE 10.6.** Frequency of home range (a) and core area (b) fidelity before and during wolf restoration, showing higher degree of fidelity of adult cougars during wolf restoration (DW,  $n = 41$ ) compared to before wolf restoration (PW,  $n = 32$ ). Fidelity was assessed using Bhattacharyya's affinity (BA, Bhattacharyya 1943; Fieberg and Kochanny 2005).



their home range with other females. The home ranges of five DW females were completely engulfed by males. Although DW males maintained smaller home ranges and overlapped more females than PW males, their home ranges overlapped with other males to a degree similar to that of PW males (table 10.5).

If cougars exclude other same-sex cougars from the core of their ranges but tolerate intrusion or defend less at the periphery, then core areas are predicted to overlap less (Creel and Creel 2001). In table 10.5 we see that inner core areas of both PW male and PW female cougars did overlap less with same-sex neighbors than did their home range boundaries [18]. This was not the case for DW females and DW males. They shared portions of their core areas with same-sex neighbors to almost the same extent as they shared the outer contours of their home ranges [19].

**TABLE 10.4.** Average number ( $\pm 1$  standard deviation) of adult cougar annual home ranges and core areas that were shared with same and opposite sex pairings in the pre-wolf (1987–94) and during wolf (1998–2005) study periods on the Greater Yellowstone Northern Range. Home ranges are 95 percent fixed kernel (FK); core areas are 50 percent fixed kernel.

| Study<br>Phase and<br>Year | Female-Female |               | Male-Male |               | Female-Male |               | Male-Female |               |
|----------------------------|---------------|---------------|-----------|---------------|-------------|---------------|-------------|---------------|
|                            | No.           |               | No.       |               | No.         |               | No.         |               |
|                            | n             | Shared        | n         | Shared        | n           | Shared        | n           | Shared        |
| PRE-WOLF (95% FK)          |               |               |           |               |             |               |             |               |
| 1989–90                    | 2             | 1.0 $\pm$ 0.0 | 2         | 1.0 $\pm$ 0.0 | 5           | 1.4 $\pm$ 0.5 | 3           | 2.3 $\pm$ 1.2 |
| 1990–91                    | 4             | 1.8 $\pm$ 1.0 | 3         | 2.0 $\pm$ 1.0 | 8           | 1.6 $\pm$ 0.5 | 5           | 3.3 $\pm$ 2.1 |
| 1991–92                    | 5             | 2.4 $\pm$ 1.5 | 2         | 1.0 $\pm$ 0.0 | 5           | 1.6 $\pm$ 0.5 | 4           | 2.0 $\pm$ 0.8 |
| DURING WOLF (95% FK)       |               |               |           |               |             |               |             |               |
| 2000–2001                  | 8             | 3.1 $\pm$ 1.8 | 1         | 1.0 $\pm$ 0.0 | 9           | 1.8 $\pm$ 0.7 | 3           | 5.1 $\pm$ 2.1 |
| 2001–2                     | 5             | 3.0 $\pm$ 1.2 | 2         | 1.5 $\pm$ 0.7 | 8           | 2.1 $\pm$ 0.4 | 3           | 5.7 $\pm$ 2.5 |
| 2002–3                     | 5             | 3.4 $\pm$ 1.7 | 2         | 1.5 $\pm$ 0.7 | 8           | 2.1 $\pm$ 0.6 | 3           | 5.7 $\pm$ 0.6 |
| 2003–4                     | 4             | 2.3 $\pm$ 1.5 | 1         | 1.0 $\pm$ 0.0 | 5           | 1.6 $\pm$ 0.5 | 2           | 4.0 $\pm$ 1.4 |
| PRE-WOLF (50% FK)          |               |               |           |               |             |               |             |               |
| 1989–90                    | 3             | 1.3 $\pm$ 0.6 | 2         | 1.0 $\pm$ 0.0 | 6           | 1.2 $\pm$ 0.4 | 3           | 2.7 $\pm$ 0.6 |
| 1990–91                    | 3             | 1.3 $\pm$ 0.6 | 2         | 2.0 $\pm$ 1.4 | 6           | 1.5 $\pm$ 0.5 | 4           | 2.3 $\pm$ 1.3 |
| 1991–92                    | 5             | 2.4 $\pm$ 1.7 | 1         | 1.0 $\pm$ 0.0 | 7           | 1.4 $\pm$ 0.8 | 3           | 3.3 $\pm$ 2.3 |
| DURING WOLF (50% FK)       |               |               |           |               |             |               |             |               |
| 2000–2001                  | 7             | 2.1 $\pm$ 1.2 | 1         | 1.0 $\pm$ 0.0 | 6           | 2.2 $\pm$ 0.4 | 3           | 4.3 $\pm$ 2.9 |
| 2001–2                     | 3             | 2.0 $\pm$ 1.0 | 2         | 1.0 $\pm$ 0.0 | 8           | 1.9 $\pm$ 0.4 | 3           | 5.0 $\pm$ 2.0 |
| 2002–3                     | 4             | 1.5 $\pm$ 1.0 | 2         | 1.0 $\pm$ 0.0 | 7           | 1.7 $\pm$ 0.8 | 3           | 4.0 $\pm$ 1.0 |
| 2003–4                     | 4             | 2.3 $\pm$ 1.3 | 1         | 1.0 $\pm$ 0.0 | 6           | 1.3 $\pm$ 0.5 | 2           | 4.5 $\pm$ 2.1 |

Comparisons between study periods revealed that same-sex and opposite-sex neighbors were likely to overlap one another to a greater degree in the DW period compared to the PW period, but most comparisons were not statistically different (table 10.5). It was only clear that females shared their home ranges and core areas with neighboring males to a much greater extent during wolf restoration than prior to wolf presence [20].

Although cougars shared a large percentage of their home range with multiple cougars, particularly during wolf restoration, the UD overlap index indicated that they shared space with other individuals very little, and they did not spend time in the same places in the areas where they did overlap. Prior to wolf restoration, male cougars shared portions of their home ranges and core areas with individual females to the same degree that females shared their ranges with each other (table 10.6) [21]. We expected differences in the degree to which DW females overlapped each other, but we found none [22]. A comparison of the distribution of overlaps revealed that DW females overlapped with a greater number of other females, but their overlap was skewed toward small amounts compared to their PW counterparts (fig. 10.7a, 10.7b). As a result, males overlapped females to a greater degree during than prior to wolf presence (fig. 10.7c, 10.7d) [23].

In summary, DW female cougars maintained home range sizes similar to those of PW females but shared a modestly greater portion of their home range and core area with a greater number of other females. During wolf, males maintained comparable territorial overlap with other male territories in spite of having smaller home ranges that overlapped more females compared to PW males.

## EFFECT OF COUGAR DENSITY AND PREY ABUNDANCE ON HOME RANGE SIZE

To test predictions of the relative influence of cougar and prey density on home range size (see chapter 9), we regressed home range size on cougar density and prey abundance. First, we used the average home range size for each individual cougar during each year and looked for relationships to female and male cougar density within home ranges within each study period. (We were unable to use elk density in these comparisons because we lacked data on elk density within individual cougar's home ranges each year.) Then, to include elk abundance, we used the average home range and core



**TABLE 10.5.** Total overlap of a cougar's home range shared by all neighboring same-sex and opposite-sex individuals before wolves (November 1990–October 1991) and during wolf restoration (November 2000–October 2001), calculated as a percentage and with the utilization distribution overlap index (UDOI). Overlap using UDOI was calculated as the overlap of each adult cougar's 95 percent fixed kernel home range with the summed 95 percent distributions of all other adults of the same or opposite sex and then rescaled to 1. UDOI overlap of 50 percent utilization distributions was calculated similarly and then rescaled to 1.

| Category of overlap      | n <sup>a</sup> | Percent Overlap |                   | UDOI          |                      |
|--------------------------|----------------|-----------------|-------------------|---------------|----------------------|
|                          |                | Mean ± SD       | Median            | Mean ± SD     | Median               |
| PRE-WOLF PERIOD          |                |                 |                   |               |                      |
| Female-female home range | 9              | 49.6 ± 17.2     | 45.0 <sup>b</sup> | 0.054 ± 0.077 | 0.022                |
| Female-male home range   | 9              | 68.1 ± 18.8     | 74.0 <sup>b</sup> | 0.066 ± 0.123 | 0.021 <sup>c</sup>   |
| Male-male home range     | 5              | 58.2 ± 27.5     | 55.0              | 0.085 ± 0.070 | 0.050                |
| Male-female home range   | 5              | 54.2 ± 24.5     | 67.0              | 0.191 ± 0.276 | 0.094                |
| Female-female core area  | 9              | 39.7 ± 30.7     | 34.0              | 0.026 ± 0.045 | 0.005                |
| Female-male core area    | 9              | 44.9 ± 26.6     | 52.0              | 0.026 ± 0.054 | 0.004 <sup>d</sup>   |
| Male-male core area      | 5              | 24.2 ± 17.5     | 18.0              | 0.018 ± 0.021 | 0.005                |
| Male-female core area    | 5              | 39.0 ± 23.0     | 41.0              | 0.066 ± 0.118 | 0.006                |
| DURING WOLF PERIOD       |                |                 |                   |               |                      |
| Female-female home range | 11             | 69.0 ± 25.9     | 69.0              | 0.077 ± 0.066 | 0.063 <sup>e</sup>   |
| Female-male home range   | 11             | 76.9 ± 23.3     | 78.0              | 0.157 ± 0.125 | 0.089 <sup>c,e</sup> |
| Male-male home range     | 5              | 54.6 ± 27.4     | 70.0              | 0.155 ± 0.138 | 0.171                |
| Male-female home range   | 5              | 59.8 ± 16.2     | 67.0              | 0.058 ± 0.035 | 0.051                |
| Female-female core area  | 11             | 55.3 ± 29.1     | 57.0              | 0.027 ± 0.027 | 0.017                |
| Female-male core area    | 11             | 63.6 ± 22.2     | 69.0              | 0.054 ± 0.054 | 0.037 <sup>d</sup>   |
| Male-male core area      | 5              | 35.4 ± 32.7     | 38.0 <sup>f</sup> | 0.058 ± 0.060 | 0.064                |
| Male-female core area    | 5              | 68.6 ± 30.2     | 79.0 <sup>f</sup> | 0.024 ± 0.013 | 0.019                |

<sup>a</sup> Sample size is number of individuals for which we had enough information to calculate total overlap.

<sup>b</sup> During the pre-wolf study, a larger portion of a female's home range area was overlapped by males than by other females ( $P = 0.100$ ), but no difference was apparent when using the UDOI as an index of overlap ( $P = 0.860$ ).

<sup>c</sup> Female home ranges were overlapped (UDOI) to a greater extent by males during wolf restoration than prior to wolf presence ( $P = 0.007$ ), yet results with percent overlap did not support differences ( $P = 0.120$ ).

<sup>d</sup> Female core areas were overlapped to a greater extent (UDOI) by males during wolf restoration than prior to wolf presence ( $P = 0.006$ ), yet results with percent overlap did not support differences ( $P = 0.211$ ).

<sup>e</sup> During wolf restoration, a female's home range area was overlapped by males to a greater extent than by other females (UDOI,  $P = 0.088$ ), but no difference was found with percent overlap ( $P = 0.670$ ).

<sup>f</sup> During wolf restoration, a larger portion of a male's core area was overlapped by females than by other males ( $P = 0.095$ ), but no difference was apparent when using the UDOI as an index of overlap ( $P = 0.531$ ).

area size of all individuals for each gender within each year and compared the relationship of these home ranges to the abundance of prey as well as to cougar and wolf density. This comparison had limitations because we had only an estimate of the relative minimum abundance of elk in the study area.

### Individual Annual Home Ranges and Cougar Density

In the prey-rich environment prior to wolf presence, we found an inverse relationship between male home range

size and the density of male cougars but a lack of relationship between home range size and cougar density in all other comparisons [24]. These findings (1) indicated that female home range size was not related to female or male density, suggesting that prey and other resources were most important; and (2) lent support to the hypothesis that males were primarily concerned with avoiding competitors or that at lower female density, males abandoned territoriality and adopted more of a roaming mating system (Sandell 1989; Goszczynski 2002; Herfindal et al. 2005).

**TABLE 10.6.** Utilization distribution overlap index (UDOI) between home ranges and core areas of pairs of adult cougars before and during wolf restoration on the Greater Yellowstone Northern Range. Home range sizes are 95 percent fixed kernel; core areas are 50 percent fixed kernel.

| Study period and pair | UDOI Overlap (95% fixed kernel) |      |      |        |      |      | UDOI Overlap (50% fixed kernel) |      |       |        |       |      |
|-----------------------|---------------------------------|------|------|--------|------|------|---------------------------------|------|-------|--------|-------|------|
|                       | N                               | Mean | SE   | Median | Min  | Max  | N                               | Mean | SE    | Median | Min   | Max  |
| <b>PRE-WOLF</b>       |                                 |      |      |        |      |      |                                 |      |       |        |       |      |
| Female-female         | 24                              | 0.09 | 0.02 | 0.06   | 0.01 | 0.38 | 20                              | 0.05 | 0.02  | 0.03   | 0.002 | 0.28 |
| Male-female           | 33                              | 0.11 | 0.03 | 0.05   | 0.01 | 0.64 | 30                              | 0.06 | 0.01  | 0.04   | 0.004 | 0.35 |
| Male-male             | 10                              | 0.05 | 0.02 | 0.02   | 0.01 | 0.20 | 7                               | 0.03 | 0.008 | 0.02   | 0.01  | 0.07 |
| <b>DURING WOLF</b>    |                                 |      |      |        |      |      |                                 |      |       |        |       |      |
| Female-female         | 73                              | 0.11 | 0.03 | 0.04   | 0.01 | 1.08 | 36                              | 0.07 | 0.02  | 0.02   | 0.002 | 0.50 |
| Male-female           | 66                              | 0.17 | 0.02 | 0.05   | 0.10 | 0.76 | 48                              | 0.08 | 0.01  | 0.05   | 0.002 | 0.38 |
| Male-male             | 6                               | 0.17 | 0.08 | 0.07   | 0.01 | 0.51 | 5                               | 0.10 | 0.05  | 0.02   | 0.01  | 0.25 |

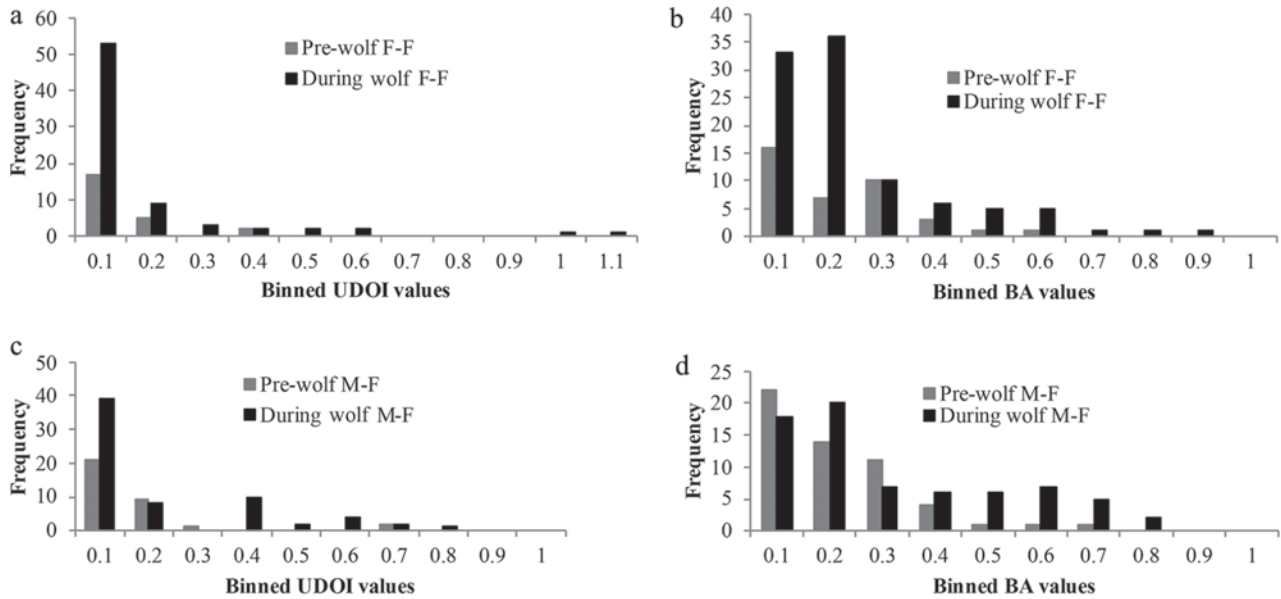
Although males may have roamed to locate low-density females in the early restoration phases, female density quickly increased. And with the exception of a few males that gradually made shifts, fidelity was strong, providing evidence against abandonment. Thus male avoidance of conspecific competitors was the most supported hypothesis during the PW period.

During wolf restoration, female and male home range size was inversely related to the density of both females and males [25]. The strongest of these relationships indicated that female home range size was tied to the density of females and declined as density of females increased. This tendency, without considering prey abundance, would be consistent with female avoidance of other females if overlap also decreased. However, we found the opposite results for overlap of female home ranges. Female overlap increased during wolf presence, indicating that either (1) the growing cougar population was filling in the best habitat up to the point of social or environmental carrying capacity, or (2) interactions with wolves were causing cougars to condense their activity into the most secure habitat. We suggest that the observed increase in female overlap was in fact a wolf effect, and we give further evidence to support this in chapters 11 and 12. Male home range size decreased with increasing densities of females more than with increasing densities of males. In summary, after cougars were restored and wolves were present, the density of cougars influenced home range sizes of female and male cougars. But were female and male home range sizes more strongly related to availability of prey? We include prey in the next section but at a coarser scale of analysis.

### Average Annual Home Ranges, Prey Abundance, and Carnivore Density

The average home range sizes of female and male cougars were not highly influenced by elk abundance or the density of combined male and female cougars in either study period, indicating a lack of support for any of the suggested hypotheses at this scale of analysis (fig. 10.8) [26]. Next we examined relationships to core areas, as they reflected the area used most intensely by cougars. In the prey-rich environment prior to wolf presence, female and male core area size was positively related to the abundance of elk (table 10.7). As elk density was increasing in the PW study, both the number of mates for male cougars and the distribution of competitors were low. Although the relationship was weaker, core area sizes of males decreased as the density of females increased. Following wolf restoration, female and male core area sizes were weakly positively related to elk abundance and bore no relationship to cougar or wolf density (table 10.7). When we looked across both study phases combined, the influence of female density on core areas of males increased in importance, while female core area sizes bore no relationship to prey, cougar, or wolf density. Collapsing data to one home range size per year may be insufficient and may not provide an adequate test of the effect of elk abundance on cougar core area size.

In summary, we found mixed support for the land tenure and two-strategies hypothesis as related to the response of the increasing density of interspecific competitors on the Greater Yellowstone Northern Range. As prey declined and cougar densities increased between the two study periods, under the two-strategies hypothesis we should have



**FIGURE 10.7.** Frequency of overlap of cougar home ranges for female-female (a, b) and male-female (c, d) dyads before and during wolf restoration on the Greater Yellowstone Northern Range, 1987–2005. Annual home ranges are 95 percent fixed kernel. Two overlap indices are used for comparison: the utilization distribution overlap index (UDOI) and Bhattacharyya's affinity (BA, Bhattacharyya 1943; Fieberg and Kochanny 2005). Values for UDOI can range from zero to greater than one, while BA values range from zero to one (see text). Because results were similar and UDOI is a preferred measure of overlap, we present test results in the text using UDOI.

observed an increase in home range size of females, with less overlap and fidelity to home ranges. Instead, home range size of females remained unchanged while overlap and fidelity increased, consistent with greater influence of conspecific and competitor densities and females sharing areas of lower prey use, as we discuss later. Male home range size declined as a result of greater social stability, greater predictability of females, and greater overlap of females, consistent with predictions for males from both the land tenure and two-strategies hypotheses.

## OVERLAP AND ACTIVITY PATTERNS OF COUGARS AND WOLVES

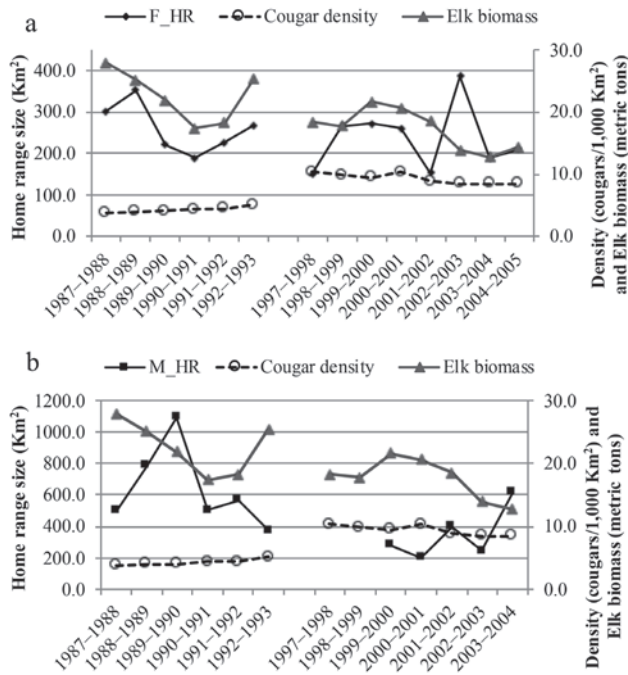
We evaluated the number of overlaps as well as total static overlap of cougar home ranges and wolf territories and their core areas to assess whether the two species were spatially segregated on the Greater Yellowstone Northern Range (Ruth 2004a; Berger and Gese 2007; Kortello et al. 2007).

Examination of static overlap, even using UDOI, provided only part of the picture of cougar and wolf use of home ranges and territories. Cougars' spatial overlap with

wolves could be offset by temporal avoidance, whereby direct encounters between cougars or between competitors were rare because neighboring individuals or packs rarely used an area of overlap at the same time. We questioned whether cougars actively avoided exploitation and interference competition by being active at different hours of the day than wolves, particularly in winter, when there was greater overlap between the two species (Arjo and Pletscher 1999; Ruth 2004a; Kortello 2005). Further, when they were located at simultaneous times, did cougars show a consistent pattern of avoiding wolves? We addressed this question by examining dynamic interactions using a set of simultaneous locations.

### Overlap of Cougars and Wolves

Our monitoring of cougars and wolves resulted in 46 measures of overlap during early wolf restoration (1998–2001) and 102 measures of overlap when wolves were colonized (2002–2005). During early wolf restoration, each adult cougar shared part of its combined summer and winter home range with an average of 4.3 and 5.6 combined summer and



**FIGURE 10.8.** Annual home range size (95 percent fixed kernel), density of adult cougars, and elk biomass on the Greater Yellowstone Northern Range, Montana and Wyoming, prior to wolves (1987–94) and during wolf restoration and colonization (1997–2005).

winter wolf pack territories, respectively (table 10.8). After wolves were colonized and more wolf packs used the Greater Yellowstone Northern Range, adult cougars shared parts of their combined summer and winter home range with an average of 5.4 and 7.7 combined summer and winter wolf pack territories, respectively (table 10.8). While as a result of their larger home ranges all male cougars overlapped a similar number of wolf territories—7.7 to 9.7 packs—adult female cougars had greater variation in the number of wolf territories they overlapped. Adult female F115 overlapped only with the Swan Lake pack, whereas adult females F107, F120, F123, and F125 overlapped with 9 to 10 combined winter wolf territories after wolves were colonized.

Using total percentage overlap and UDOI, we examined total static overlap between adult cougars and wolves for 2001–2002 and 2002–2003, the years we had the greatest proportion of marked cougars. As we expected, during these two years a cougar's home range was overlapped considerably—58 percent to 93 percent (95 percent confidence intervals of total percentage overlap)—by multiple wolf packs

(2–10). Home ranges of four females and one male cougar were completely subsumed within multiple wolf territories. We expected that the core areas would provide the best evidence as to whether cougars were able to segregate themselves spatially from wolves. Contrary to our prediction that cougar and wolf core areas would overlap very little, the total percentage of a cougar's core area shared with wolf packs was slightly larger—at 70 percent to 98 percent for all cougars—than overlap of their 95 percent home ranges. Core areas of seven females and two males were subsumed within multiple wolf territories.

This considerable overlap of cougar home ranges and wolf territories suggested no direct evidence of competitive avoidance. Yet while wolf packs overlapped a high total percentage of each cougar's home range and core area, UDOI values revealed that cougars and wolves did not use shared areas in a similar manner (table 10.8). During summer, home range overlap between paired cougar and wolf packs reflected a low degree of sharing, and the magnitude of sharing in summer did not increase as wolves transitioned from restoration to colonization [27]. As expected, cougar and wolf overlap increased in winter compared to summer; further, winter UDOI overlap increased as wolves transitioned from restoration to colonization (table 10.8; see also Ruth 2004a) [28]. As wolves were restored, four of eleven cougars overlapped one to two wolf packs with UDOI greater than 1.0. As the number of wolf packs grew and wolves became colonized on the Northern Range, the number of cougars overlapping at least one pack with UDOI greater than 1.0 jumped to ten of sixteen. If areas of home range overlap hold the greatest densities of prey, then risk of encountering wolves may not outweigh the need for cougars to access areas containing food. We return to this idea in chapter 11 when we look more closely at the spatial-habitat changes of cougars.

Despite some cougars sharing substantial portions of their home ranges with multiple wolf packs during summer and winter periods, the areas they used most intensively—their core areas—had very little overlap with core areas of multiple packs. In other words, core areas of cougar use were typically situated away from areas used most intensively by wolves during both seasons. Even when they did overlap to some degree, the two carnivores were not spending time in the same places very often, suggesting that cougars avoided wolves (table 10.8). For example, after wolves were colonized, female cougar F47's combined winter home range



**TABLE 10.7.** Relationship of female and male cougar core area size to prey abundance, cougar density in the study area (SA), cougar density within the core area of all cougars (1987–2004), and wolf density before and during wolf restoration on the Greater Yellowstone Northern Range, Montana and Wyoming. Pre-wolf = 1987–95; during wolf = 1998–2005; relationships are from linear regression analyses; core areas are 50 percent fixed kernels.

| Study Period          | Female Cougars |       |       |         |                       | Male Cougars |       |       |         |
|-----------------------|----------------|-------|-------|---------|-----------------------|--------------|-------|-------|---------|
|                       | AICc           | ΔAICc | R2adj | P-Value |                       | AICc         | ΔAICc | R2adj | P-Value |
| PRE-WOLF              |                |       |       |         | PRE-WOLF              |              |       |       |         |
| All elk               | 42.53          | 0.0   | 44.4  | 0.09    | Adult elk             | 62.22        | 0.0   | 70.8  | 0.02    |
| Female core           | 43.75          | 1.2   | 6.1   | 0.14    | Female core           | 63.30        | 1.1   | 64.9  | 0.03    |
| Female SA             | 43.75          | 1.2   | 6.1   | 0.14    | Female SA             | 63.30        | 1.1   | 64.9  | 0.03    |
| Adult elk             | 44.68          | 2.1   | 3.6   | 0.20    | Male SA               | 65.65        | 3.4   | 48.1  | 0.08    |
| Male core             | 47.02          | 4.5   | 6.1   | 0.64    | Male core             | 65.65        | 3.4   | 48.1  | 0.08    |
| Male SA               | 47.02          | 4.5   | 6.1   | 0.64    | All elk               | 66.22        | 4.0   | 42.9  | 0.09    |
| Elk calves            | 47.12          | 4.6   | 4.5   | 0.69    | Elk calves            | 67.68        | 5.5   | 27.2  | 0.17    |
| DURING WOLF           |                |       |       |         | DURING WOLF           |              |       |       |         |
| Adult elk             | 47.65          | 0.0   | 21.9  | 0.20    | All elk               | 49.51        | 0.0   | 41.2  | 0.15    |
| All elk               | 48.57          | 0.9   | 8.8   | 0.29    | Adult elk             | 49.59        | 0.1   | 40.3  | 0.15    |
| Male core             | 50.13          | 2.5   | 0.1   | 0.95    | Female core           | 50.13        | 0.6   | 3.8   | 0.36    |
| Male SA               | 50.13          | 2.5   | 0.1   | 0.95    | Female SA             | 50.13        | 0.6   | 3.8   | 0.36    |
| Elk calves            | 50.32          | 2.7   | 2.4   | 0.77    | Elk calves            | 51.92        | 2.4   | 4.9   | 0.35    |
| Wolf density          | 50.41          | 2.8   | 0.0   | 0.85    | Wolf density          | 53.60        | 4.1   | 0.0   | 0.96    |
| Female core           | 50.46          | 2.8   | 5.5   | 0.65    | Male core             | 53.60        | 4.1   | 0.0   | 0.97    |
| Female SA             | 50.46          | 2.8   | 5.5   | 0.65    | Male SA               | 53.60        | 4.1   | 0.0   | 0.97    |
| STUDY PHASES COMBINED |                |       |       |         | STUDY PHASES COMBINED |              |       |       |         |
| Adult elk             | 423.37         | 0.0   | 10.3  | 0.31    | Female SA             | 414.92       | 0.0   | 69.3  | 0.002   |
| All elk               | 423.56         | 0.2   | 8.9   | 0.35    | Female core           | 417.09       | 2.2   | 62.6  | 0.003   |
| Male SA               | 424.38         | 1.0   | 2.4   | 0.63    | Male core             | 420.05       | 5.1   | 51.1  | 0.01    |
| Female SA             | 424.52         | 1.1   | 1.3   | 0.74    | Male SA               | 420.69       | 5.8   | 48.1  | 0.01    |
| Male core             | 424.64         | 1.3   | 0.3   | 0.87    | Adult elk             | 421.91       | 7.0   | 42.1  | 0.02    |
| Female core           | 424.66         | 1.3   | 0     | 0.93    | All elk               | 424.44       | 9.5   | 27.1  | 0.06    |
| Elk calves            | 424.67         | 1.3   | 0     | 0.96    | Elk calves            | 428.75       | 13.8  | 2.9   | 0.62    |

overlapped with eight wolf packs: the Geode Creek, Buffalo Plateau, Specimen Ridge, Agate, Druid, Slough Creek, Leopold, and Tower Creek packs. Yet F47's combined winter core area was situated so that she barely overlapped four of those packs' core areas—she overlapped the core area of the Geode Creek, Buffalo Plateau, and Slough Creek packs with UDOI of 0.1 and the Agate pack with UDOI of 0.01 (fig. 10.9). With the exception of female cougar F163, this pattern was consistent across all cougars, so that cougar core areas overlapped with wolf core areas an average of 32 percent less than the number of home range overlaps, and UDOI values were quite low, ranging from 0.01 to 0.22. Only female

cougar F163 had high overlap of her core area with that of a single wolf pack. Her cumulative winter home range overlapped a total of nine packs, and overlap with the Rose2 pack was greatest—a UDOI of 3.7—indicating high potential for encounter. F163's core area overlapped only with the Rose2 core area and not at all with those of any of the other packs. With a UDOI overlap of 0.88, F163's core area overlap with the Rose2 pack core was more substantial than any other cat's core area overlap with wolves. This overlap was possibly a result of the Rose2 pack fading from existence at this time, and they perhaps were no longer moving as a cohesive pack, resulting in a larger area of use.

**TABLE 10.8.** Overlap (utilization distribution overlap index, UDOI) for adult cougar combined summer and winter home ranges with wolf combined summer and winter home ranges during early wolf restoration and wolf colonization periods on the Greater Yellowstone Northern Range, 1998–2005.

| Study Period and Overlap Range         | No. Shared           |           | Overlaps <sup>b</sup> | Mean | UDOI Overlap |        |      |      |
|----------------------------------------|----------------------|-----------|-----------------------|------|--------------|--------|------|------|
|                                        | Cougars <sup>a</sup> | Mean ± SD |                       |      | SE           | Median | Min  | Max  |
| COMBINED HOME RANGE (95% FIXED KERNEL) |                      |           |                       |      |              |        |      |      |
| Wolf restoration                       |                      |           |                       |      |              |        |      |      |
| Summer                                 | 11                   | 4.3 ± 0.9 | 23                    | 0.44 | 0.09         | 0.27   | 0.02 | 1.68 |
| Winter                                 | 7                    | 5.6 ± 0.5 | 23                    | 0.65 | 0.06         | 0.51   | 0.07 | 2.25 |
| Wolf colonization                      |                      |           |                       |      |              |        |      |      |
| Summer                                 | 16                   | 5.4 ± 2.4 | 49                    | 0.47 | 0.06         | 0.34   | 0.04 | 2.17 |
| Winter                                 | 15                   | 7.7 ± 2.7 | 53                    | 0.92 | 0.11         | 0.63   | 0.10 | 3.74 |
| COMBINED CORE AREA (50% FIXED KERNEL)  |                      |           |                       |      |              |        |      |      |
| Wolf restoration                       |                      |           |                       |      |              |        |      |      |
| Summer                                 | 6                    | 1.2 ± 0.4 | 7                     | 0.04 | 0.01         | 0.03   | 0.01 | 0.09 |
| Winter                                 | 6                    | 2.0 ± 0.9 | 12                    | 0.05 | 0.02         | 0.03   | 0.01 | 0.22 |
| Wolf colonization                      |                      |           |                       |      |              |        |      |      |
| Summer                                 | 9                    | 1.4 ± 0.9 | 13                    | 0.07 | 0.02         | 0.09   | 0.01 | 0.19 |
| Winter                                 | 12                   | 2.6 ± 2.0 | 31                    | 0.10 | 0.03         | 0.05   | 0.01 | 0.88 |

<sup>a</sup> Number of individual cougars sharing areas with other cougars.<sup>b</sup> Number of total overlaps.

### Daily Activity of Cougars and Wolves

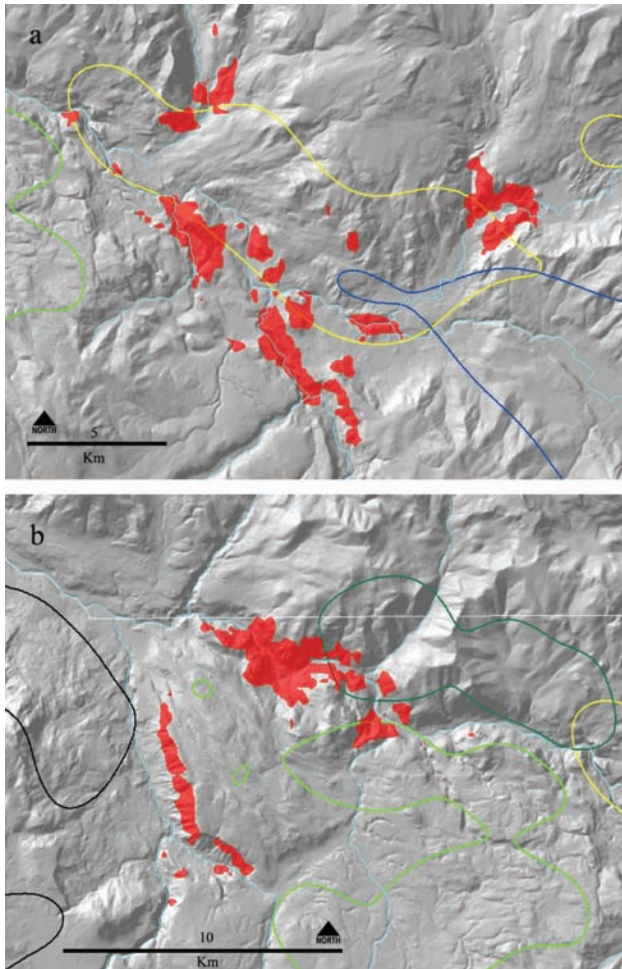
We used 10,074 GPS locations collected at three-hour intervals from collars on ten cougars in the wolf restoration study and 4,303 GPS locations on seven wolves in four packs overlapping GPS-collared cougars to compare timing of activity and rates of movement of the two carnivore species.

On the Greater Yellowstone Northern Range, cougars and wolves were overwhelmingly crepuscular and nocturnal, reflecting largely similar patterns of activity (figs. 10.10 and 10.11). Activity of female cougars peaked between 1700 and 2100 hours as well as between 0000 and 0600 hours during both seasons (figs. 10.10a and 10.11a). Male cougars also had corresponding peaks in activity in winter and summer. Like females, males were most active between 1700 and 2100 hours, with activity peaking again at 0000 to 0200 hours (figs. 10.10b and 10.11b). Wolves had few distinct peaks in activity in winter. During the evening and night from 1800 to 0600 hours, wolves were more consistently active in summer (figs. 10.10c and 10.11c). Apparently, cougars were not avoiding activity at times when wolves were also most active. The peak in activity of cougars and wolves was consistent with the hypothesis that predators track the activity periods of their primary prey (Curio 1976; Beier et al. 1995).

Cougars killed prey most commonly at night, while locations associated with bed sites or other signs were more likely to occur during the day (Ruth et al. 2010). Hence 73 percent of large ungulate kills and 64 percent of small ungulate kills occurred between the hours of 2000 and 0500 (Ruth et al. 2010). The greater time cougars spent feeding at kills than wolf packs spent at kills may be reflected in the very limited movements—10 to 129 meters per hour—for cougars between 2100 and 2300 hours, times when cougars often made kills (figs. 10.10 and 10.11; Beier et al. 1995; Ruth et al. 2010).

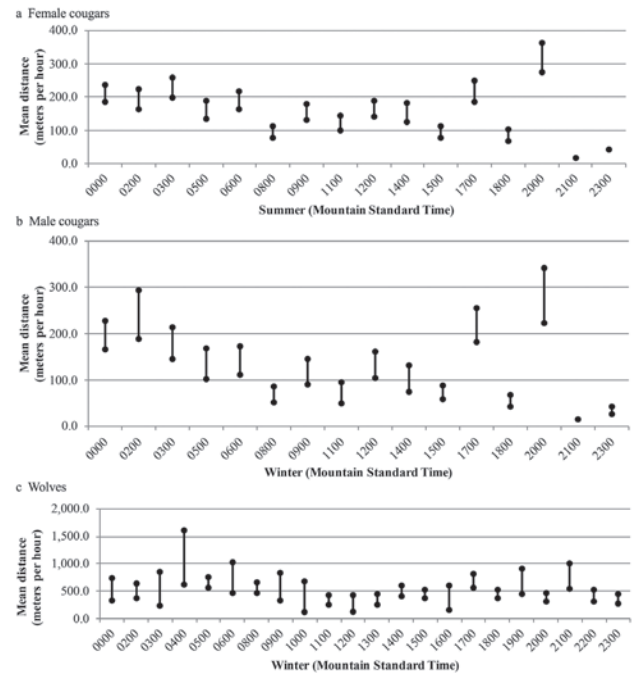
### Movement Rates in Areas of Greatest Risk

Regardless of the time of day, wolves generally covered greater distances than cougars. Wolves traveled at two to twelve times the rate of female and male cougars across winter and summer landscapes, although these movements differed most greatly from the winter morning travel of rather sedentary male cougars (table 10.9) [29]. These larger movements were consistent with adaptations of wolves to cover ground quickly as well as with their greater energetic needs as a pack (fig. 10.12; chapter 8; Kreeger 2003; Peterson and Ciucci 2003). During their summer evening and nighttime



**FIGURE 10.9.** Orientation of adult female cougar core areas relative to wolf pack core areas in early winter on the Greater Yellowstone Northern Range. *a*: Female cougar F47's core area (red) and the Leopold (light green), Geode (yellow), and Rose Creek (blue) wolf packs, early winter, 1998–2001. *b*: Female cougar F106's core area (red) and the Leopold (light green), Geode (yellow), Swan Lake (black), and Agate (dark green) wolf packs, early winter, 1999–2001. Although cougars shared substantial portions of their home ranges with multiple wolf packs during summer and winter periods, the areas they used most intensively—their core areas—had very little overlap with core areas of multiple packs. The core area depicted for both females is based on a synoptic model of spatial-habitat use (see appendix E and F); wolf pack core areas are 50 percent fixed kernel.

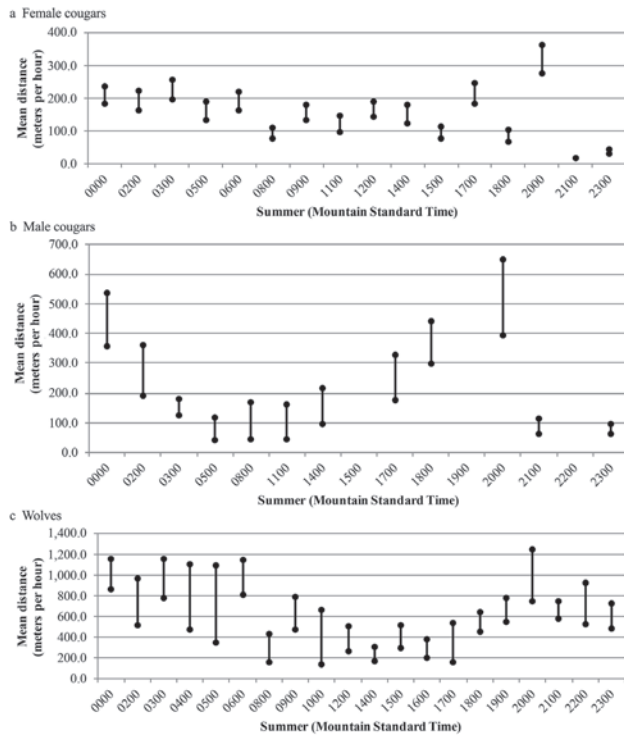
travels across the Greater Yellowstone Northern Range, wolves moved at a maximum speed of 5 km/hour. While felids are not adapted to prolonged rapid movement, cougars were capable of covering a little over 2 km/hour at



**FIGURE 10.10.** Mean distance traveled between GPS locations for cougars and wolves during winter on the Greater Yellowstone Northern Range, 2001–2006. Female cougars (*a*;  $n = 3,470$  locations, from 5 females); male cougars (*b*;  $n = 1,022$  locations, from 5 males); wolves (*c*;  $n = 2,188$  locations, from 7 wolves in 4 packs). We constrained data to 3-hour location intervals for cougars and 2-, 3-, and 4-hour location intervals for wolves, and time periods with fewer than 16 locations were removed.

the maximum observed speed for both males and females. Researchers in west-central Alberta also reported that wolves were most active at dawn and dusk and moved nearly three times as fast as cougars, while cougar movement rates peaked during the evening (Webb et al. 2011).

With cougars and wolves active at similar times and wolves covering ground at a greater rate than cougars, we questioned whether movements of cougars might differ when they were in the most secure part of their home range compared to when they traveled outside this core area. When female cougars were outside their core areas at night, whether in the core or the periphery of wolf territories, they traveled more quickly than they did inside their core areas [30]. Cougars were more likely than wolves to make kills within their core areas, where risk of encounter with wolves was probably less. As a consequence, localization



**FIGURE 10.11.** Mean distance traveled between GPS locations for cougars and wolves during snow-free months on the Greater Yellowstone Northern Range, 2001–6. Female cougars (a;  $n = 4,656$  locations, from 5 females); male cougars (b;  $n = 926$  locations, from 5 males); wolves (c;  $n = 2,115$  locations, from 7 wolves in 4 packs). We constrained data to 3-hour location intervals for cougars and 2-, 3-, and 4-hour location intervals for wolves, and time periods with fewer than 16 locations were removed.

at kills probably translated to slower movements because cougars spent more time at kills than did wolves. However, after wolves were restored on the Northern Range, risks were likely greater when female cougars were traveling at night outside their own core areas. Rapid movements could signify more cautious or flight behavior in areas of high risk at a time when wolves were likewise most active—at night. Rapid movements could also indicate bouts of hunting by cougars in areas outside their core areas, but our previous findings ran counter to this idea.

Unlike female cougars in our study area, male cougars typically did not move at different rates when they were in their core areas compared to traveling outside core areas. Instead, during the day in winter, males traveled at a significantly slower rate through the core area of wolves com-

**TABLE 10.9.** Mean movement rates (meters per hour) and 95 percent confidence intervals of ten adult cougars and seven wolves in four packs during wolf restoration and colonization of the Greater Yellowstone Northern Range, Montana and Wyoming, 1998–2005.

| Species        | n     | Winter |                     | Summer |       |                     |
|----------------|-------|--------|---------------------|--------|-------|---------------------|
|                |       | Mean   | Confidence Interval | n      | Mean  | Confidence Interval |
| MALE COUGARS   |       |        |                     |        |       |                     |
| Morning        | 58    | 43.8   | 25.9–61.7           | 21     | 100.7 | 5.6–195.8           |
| Midday         | 120   | 41.6   | 27.7–55.5           | 189    | 313.0 | 260.8–365.2         |
| Evening        | 152   | 333.1  | 274.7–391.5         | 56     | 711.0 | 550.9–871.1         |
| Night          | 277   | 264.0  | 218.5–309.5         | 165    | 404.5 | 328.5–480.5         |
| FEMALE COUGARS |       |        |                     |        |       |                     |
| Morning        | 344   | 107.5  | 84.8–130.2          | 446    | 149.6 | 128.5–170.7         |
| Midday         | 709   | 103.0  | 88.8–117.2          | 1,286  | 150.7 | 139.0–162.4         |
| Evening        | 388   | 122.0  | 103.0–141.0         | 187    | 431.0 | 377.8–484.2         |
| Night          | 1,093 | 217.8  | 199.2–236.4         | 1,390  | 223.1 | 207.9–238.3         |
| WOLVES         |       |        |                     |        |       |                     |
| Morning        | 182   | 555.8  | 472.6–639.0         | 153    | 489.8 | 385.8–593.8         |
| Midday         | 669   | 404.2  | 363.4–445.0         | 664    | 370.5 | 328.2–412.8         |
| Evening        | 328   | 553.3  | 486.3–620.3         | 535    | 716.0 | 645.3–786.7         |
| Night          | 1,011 | 492.5  | 451.3–533.7         | 794    | 833.3 | 768.0–898.6         |

pared with when they were moving through the periphery of wolf territories and cougar home ranges [31]. Cougars apparently adjusted behaviors depending on the magnitude of risk as well as distance to and availability of secure habitat. Thus when males were subject to higher risk in competitors' territory, they perhaps traveled more cautiously while remaining in secure rough terrain, for which males selected more strongly in winter than did female cougars (see chapter 11). When cougars entered a residential area in Arizona, their movements tended to accelerate, which might signify flight behavior (Arundel et al. 2007). Yet the slower and less angular movements of cougars in the same study suggested more cautious behavior when they approached roads and highways—areas they typically avoid. Because males are not protecting young as females do, they may adopt different strategies from those of females to avoid encounters with competitors.

### Dynamic Interactions

How did cougars respond to the presence of wolves at a finer scale and at similar times, thus more dynamically?





**FIGURE 10.12.** *Nez Perce pack on the move. Wolves can cover great distances each day when traversing territories that are roughly one and a half times larger than cougar home ranges—consistent with adaptations of wolves to cover ground quickly as well as with their greater energetic needs as a pack. Photo by Dan Stahler, National Park Service.*

To address this question we used simultaneous locations to evaluate avoidance, attraction, or random response to wolves by individual cougars. We defined simultaneous locations as those cougar and wolf VHF locations obtained within one hour of each other from fixed-wing aircraft or on the ground ( $n = 690$  locations from fifteen cougars and ten wolf packs; Logan and Sweanor 2001; Ruth 2004a; Kortello et al. 2007). In addition, we used 1,105 simultaneous GPS locations on ten adult female and five adult male cougars for which collars collected locations at the same time as GPS collars worn by seven Northern Range wolf packs. We calculated a mean observed distance between simultaneous locations of cougars and wolf packs for which 95 percent of territories (UDOI values  $>0$ ) overlapped with a cougar's home range. We compared the mean observed distance to that expected by chance. We derived expected distances by averaging distances between locations from one animal and all non-simultaneous locations from the other animal. We considered dynamic pairings to indicate that cougars avoided wolves if observed distances were greater than expected and that cougars were attracted to wolves if observed distances

were less than expected (Arjo and Pletscher 1999; Ruth 2004a; Kortello et al. 2007). If observed distances were equal to those expected by chance, cougars responded to wolves in a random manner.

Ruth (2004a) found that cougars and wolves used areas of overlap more than expected, perhaps because those areas were important for hunting prey. White and colleagues (1994) similarly proposed that coyotes and foxes used overlap areas more than expected because prey were more abundant in those areas. Yet on the Greater Yellowstone Northern Range, we found no pattern that cougars contending with a greater number of wolf packs and greater overall spatial overlap with wolves were more likely to show attraction. During summer, spatial proximity in overlapping territories was random for nine of twelve cougars, whereas two cougars were located closer to wolves than expected and one cougar (female F125) clearly avoided wolves [32]. During winter, spatial proximity of cougars and wolves was also mostly random and consistent with findings for cougars and wolves during winter in two other studies (Ruth 2004a; Kortello et al. 2007) [33]. Despite the considerable spatial overlap of

cougar and wolf territories, analysis of simultaneous telemetry observations indicated that some cougars avoided wolves while others did not appear to do so, a point we address further in chapter 11.

These analyses were not without limitations. First, the scale of this analysis and the data we had available for comparisons were perhaps insufficient to test dynamic patterns of association effectively. Although we found seven cougars closer to wolves than expected, distances overall were far apart—less than 1 percent of simultaneous locations were within 1 km, 26–35 percent were within 10 km, and the remainder were over 10 km apart. Detection and avoidance of wolves by cougars might occur at shorter distances than those that could be detected with telemetry locations within one hour of each other (see also White et al. 1994; Kortello et al. 2007). Second, although we documented direct interactions associated with eight cougar mortalities caused by wolves, nine documented cases of wolves chasing cougars not associated with displacements from kills, and twenty-seven wolf displacements of cougars from their kills, we lacked simultaneous location information for time periods leading up to these occasions. Despite our finding that spatial proximity of cougars and wolves was either random or showed attraction during winter, our later analyses indicate that cougars clearly avoided wolves during winter and were less likely to do so in summer. Cougars may do well at using areas where wolf use is already low, so most distances reflect this avoidance.

### WHAT INFLUENCED COUGAR SPATIAL STRUCTURE BEFORE AND DURING WOLF RESTORATION?

We find some support for predictions from each of the three hypotheses describing cougar spatial structure, indicating that the controls on cougar spatial structure are likely not static but rather depend on the interaction of, at the very least, cougar population density, prey abundance, and the density of competitors. A decrease in prey density that makes food difficult to find typically results in increased home range sizes, which has been shown to occur in home range sizes of both bobcats and North American and Eurasian lynxes (Ward and Krebs 1985; Litvaitis et al. 1986; Caro 1994: 220; Herfindal et al. 2005). This certainly was the case for wolf packs occupying the prey-rich Northern Range, as they tended to have the smallest territories, averaging 293 km<sup>2</sup> ( $n$

= 56), while packs occupying areas where prey was less abundant had larger territories, averaging 880 km<sup>2</sup> ( $n$  = 52; Smith and Bangs 2009).

In our study area relative prey availability—numbers and calf:cow ratios—was greatest during the PW period, with availability declining in the DW restoration period. Thus home ranges, particularly of female cougars, should have been smaller in the PW study compared to during wolf presence. Yet we found no indication that home ranges or core areas of females increased as prey declined. Logan and Sweanor (2001) hypothesized that such results would indicate that females were exhibiting a degree of avoidance of one another. As prey densities declined during wolf restoration, the inverse relationship between female home range size and the density of females suggested such avoidance, but overlap of female home ranges increased, suggesting otherwise—less avoidance and greater sharing of resources, particularly in the periphery of home ranges. We suspect that these differences were the result of: (1) the patchiness of prey on the Greater Yellowstone Northern Range and (2) cougars, in avoiding wolves, being constrained to secure habitat, which did not necessarily correspond to high prey abundance.

When food resources are clumped and patchily distributed, either spatially or temporally, cougars may benefit more by tolerating overlapping between their home ranges and those of neighbors; in that context they are benefiting by utilizing food resources without risking the costs of continued resource defense or of searching for another patch of food (Tsukada 1977; Mills 1978). In the Serengeti, cheetah ranges expanded at low prey density, but it was the patchiness of prey that accounted for expanded ranges, not low prey density (Caro 1994). Where patches of prey were variable in density, female cheetahs showed overlap, with several of them working the same high-density patch, a finding that similarly occurred with ranges of female lynxes (Ward and Krebs 1985; Caro 1994: 220).

Greater overlap of cougar home ranges could also be explained by cougar avoidance of wolves resulting in the cats being constrained to secure habitats, which did not necessarily correspond to areas of high prey abundance. Because prey declined without a corresponding increase in female home range size, prey did not appear to be a limiting resource during our study. This last outcome might also have occurred if females simply switched to preying on alternate or second-

ary prey, such as mule deer and bighorn sheep, but this was not the case. Elk accounted for a consistently large percentage of all prey killed during both periods, and cougars did not switch to an alternate or secondary prey, supporting the notion that elk were not a limiting resource during our study.

Prior to wolves, home ranges and core areas of female cougars were tied to abundant resources, overlapped less, and shifted more, probably because they did not yet have to share resources—habitat or hunting areas—to the degree that DW cougars did. As prey declined and wolves increased in number, home ranges of female cougars did not increase, but they did overlap more as cougars became constrained to the most secure habitats in the study area (see chapter 11). Although male home range size should be less related to prey than to females, in the prey-rich environment prior to wolves, male cougar home ranges and core areas were twice as large as those of DW males. Prior to wolf restoration, abundant prey and low density of female and male cougars enabled males to maintain large shifting yet distinct territories that overlapped little.

These results fit with predictions by Hornocker (2010) and findings from other studies where restoration of carnivores was taking place (Fritts and Mech 1981; Mech and Boitani 2003b). The greatest shifts in wolf pack territories occurred during the colonizing phase, probably because of the lack of constraint by any neighboring packs (Mech and Boitani 2003b). Annual home range sizes of wolves on the Greater Yellowstone Northern Range varied from 29.6 km<sup>2</sup> in year six (2002–2003) of our study, when wolf density was highest and prey density lowest, to 1,556.3 km<sup>2</sup> in the first year of our study (1997–1998), only one year after wolves were released from pens (Smith and Bangs 2009).

As the cougar population grew prior to wolf restoration, male home ranges declined as male density grew and social stability increased. Further, core areas of male cougars shrank as access to females increased (i.e., increased density of females), but core areas remained weakly tied to prey availability, apparently because female home ranges and core areas were tied to access to prey. These findings suggested to us that male cougars in the PW study were responding primarily to avoiding other male cougars while also seeking access to females. In Montana, Robinson and DeSimone (2011) found that home range sizes of male cougars were larger when there was high turnover in males during a period of heavy hunting, with home range sizes becoming smaller

after hunting ceased. In addition, during the period of heavy hunting in the same Montana study, when prey should have been more available to a lower number of female cougars, contrary to predictions female home range sizes instead grew, although overlap with other females did not change.

As wolves were restored in our study area, home ranges of male cougars declined further, as a result not only of a greater number of female cougars but of females also being more predictable on the landscape. This was in contrast to the prediction that as prey availability dropped, female home ranges should increase and become less predictable. Although cougars were highly overlapped with wolves, they avoided wolves by situating their core areas away from those of wolves, suggesting that they were also spatially constrained to the best cat habitat, which we explore further in chapter 11. Although prey were less abundant and more patchily distributed than prior to wolves, they were not yet limiting.

## SUMMARY

Changes in size, fidelity, and overlap of cougar home ranges were influenced in complex ways by intraspecific relationships, prey abundance, and avoidance of wolves—countering some predictions and supporting others. In the PW study period, home ranges of males were large, with less fidelity in home ranges by both male and female cougars. As cougar numbers and stability in social structure increased after wolf restoration, home ranges of females remained consistent in size but overlapped more with those of other females; home range sizes of males dropped to near half the size of PW home ranges of males, yet overlapped with more females; and both female and male fidelity to home ranges and core areas increased. During wolf restoration, cougars avoided areas of high wolf concentration, as seen by their establishment of core areas outside wolf core areas. However, this spatial instability in response to wolves was less than the spatial instability observed in the PW period, when the cougar population was growing and individuals had not yet established permanent home ranges. During high prey density and low carnivore density, home ranges and core areas of female cougars were mostly prey-driven and secondarily socially driven. While males avoided other males, their home ranges also reflected access to females and prey. As the density of cougars, wolves, and bears increased and elk declined, conspecifics more strongly



influenced home range sizes of females and males and elk less so, probably because elk were less abundant and more patchily distributed.

In chapter 11 we present a clearer picture of what landscape features and interspecific interactions predicted the

probability of use by cougars within the study area and within home ranges. We examine more closely the hypothesis that in avoiding wolves, cougars were constrained to secure habitat, which did not necessarily correspond to high prey abundance.

### Text Box 10.1. Shifting Ranges

In the PW period, six females showed strong shifting tendencies—with fidelity values of 0.31 to 0.45—between consecutive annual periods. Females F5, F16, F32, and F49 all shifted, apparently to accommodate philopatric daughters. It was not clear why females F9 and F35 made shifts, but the timing of F9's shift was coincident with when an unmarked kitten should have become independent from her mother. During wolf restoration, females maintained strong fidelity to home ranges, including two females that accommodated philopatric daughters without substantially shifting their home range. We observed only two of twelve females that clearly shifted home ranges during the time wolves were recolonizing the Northern Range—F105 in 1999–2000 to 2000–2001 and F107 during summer 2004. No clear pattern emerged as to why F105 shifted slightly. We suspect that F107 shifted her home range because while she was rearing kittens, conditions became unfavorable. She lost two litters of kittens—one litter of four to wolves in winter 1999 and the other litter of three to starvation as she traveled from her summer to her winter range in 2004. Prior to and during these events, F107 consistently summered in Slough Creek, west into Soda Butte Creek, and in Amphitheatre Basin. Although she also successfully raised kittens from two litters while in this summer range (two kittens during 2000–2001 and two of four kittens during 2002–3), her overlap with wolves and the heightened risk of wolf encounter during travels from summer to winter range probably prompted her to move. In 2003, F107 denned and produced a litter of three kittens very late in the year—November 22—and not until late December did she begin to move them from her summer range in the Soda Butte–Amphitheatre area, traveling along the Lamar River corridor and down to her winter range along the Yellowstone

River around Oxbow, Big Cottonwood, and Blacktail Deer Creeks. With snows accumulating, the lower-elevation route she traveled was in or near areas frequented by wolves, and travel for kittens at ten weeks old seemed difficult through the deep, unconsolidated snow present at the time. This litter of kittens succumbed to starvation between January 25 and 31, 2004, when they were thirteen and fourteen weeks old. After losing this litter, F107 remained on her winter range centered around Hellroaring Creek and established a summer range overlapping this area. She remained in her new summer range—situated ~27 km to the west of her original summer range—and produced two separate litters, in June 2004 and June 2006. She was perhaps able to abandon her summer range completely and make such a significant change because of the death of female F17 in August 2002, which left the Hellroaring area vacant.

Prior to wolves, three male cougars—M8, M28, and M36—shifted in response to the deaths of neighboring males during the hunting season to the north of Yellowstone National Park. For instance, male M8 was first captured in Slough Creek as a four-year-old resident adult. Over the next six to seven years, he shifted approximately 49 km north and east, eventually ending up 23 km north of Yellowstone National Park by Emigrant Gulch. First captured as a five-year-old adult, male M28 had an early home range that included a large area. He gradually shifted approximately 37 km and concentrated at the northern end of his range when he was seven to eight years old. During wolf restoration, seven-year-old male M131 abandoned his home range overlapping the Yellowstone River south of Tower Falls and shifted approximately 13 km to the northwest in summer 2005. Male M131 was subsequently killed by hunters outside the park in December 2006.



## CHAPTER 11

### Patterns of Resource Use Prior to and during Wolf Restoration

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The management and conservation of carnivores is largely dependent on our ability to understand and predict habitat relationships at several spatial and temporal scales (Paquet and Hackman 1995). Within their home range, cougars selectively use certain habitats more than others, and home ranges can vary seasonally, such as when cougars follow migrating prey to winter or summer ranges or during breeding (Pierce et al. 1999; Logan and Sweanor 2001; Ruth 2004a). Because of an ultimate association with food and escape cover, cougar habitat selection is typically assessed for environmental characteristics such as plant species composition, vegetation structure, and topography (Morrison et al. 1998). Yet the presence or absence of other animals may also affect space use, with avoidance and attraction usually related to mating opportunities (Emlen 1973), predator-prey relationships (Mech 1977a; Murray et al. 1994), or competition (Pimm and Rosenzweig 1981; Maurer 1984; Morris 1987; Minta 1992). Identifying resources cougars selected within the Greater Yellowstone Ecosystem and the resources selected within their home ranges was an important aspect of understanding variation in how the cats used space before and during wolf restoration.

#### DETERMINING RESOURCE USE PATTERNS

Animals make decisions about resources at hierarchical stages (Horne et al. 2008). In locating a home range in one part of the Greater Yellowstone Ecosystem, a cougar evaluates the resources and hazards of various parts of the landscape (i.e., *second-order selection*; Johnson 1980; Aebischer et al. 1993; Dickson and Beier 2002). Once the home range is established, a cougar's day-to-day movement and selection of sites are constrained by resource availability within that home range (i.e., *third-order selection*). These two levels

reveal important aspects about patterns of resource use. For example, a cougar may establish its home range where there is abundant escape cover, yet show selection for sites farther from escape cover than what is available within the home range because the overall habitat is already fairly secure.

To test whether cougars made adjustments in where they located home ranges in the study area during wolf restoration compared to their pre-wolf counterparts (i.e., *second-order selection*), we used logistic regression (Hosmer and Lemshow 2000). We used an equal number of locations across individuals within each study phase, with PW cougars serving as the reference category. Because our study area had the same defined boundary for both study phases, we were able to compare how cougars used the study area in one step instead of running separate study phase logistic regressions and then comparing the results. This also avoided the problem of having to define available resources, as we compared used habitats in one study phase to used habitats in the other study phase. But might cougars use prime habitats, defined by their core home ranges, differently from the peripheral area where overlap with wolves was greatest? To test this we grouped locations by whether they occurred in a cougar's core area (within an individual's 50 percent home range contour) or in the periphery (outside the 50 percent home range contour) and again used logistic regression to compare resource use between the two study phases in core areas and then in periphery areas.

To assess resource use within the home range (i.e., *third-order selection*) and understand changes in cougar space use before and after the restoration of wolves, we used a synoptic approach that allowed for simultaneous estimation of home ranges, resource selection, and the influence of other species (Horne et al. 2008). Briefly, the synoptic model

starts with some null model of space use that describes how an individual animal would use space if habitat conditions were irrelevant—for example, a circular pattern for an animal that has a den site to which it returns on a regular basis. Environmental features, or explanatory variables, that are predicted to affect space use then are added, making the probability of space use (pursuing the denning example) a combination of the animal's tendency to use one area and the environmental features of that area. The effects of the environmental features can then be compared across individuals and populations to assess differences in resource selection.

We realized that some cats would be more heavily affected by overlap with wolves than would others. As a result, we expected that not all cats would respond equally to the landscape or to elk and wolves. Because the individual is the sampling unit in the synoptic model approach, we were able to account for this variation. We first assessed space use for each individual cat and later combined this individual information for all cats to create a population-level picture of spatial-habitat use for each of the study periods, which we describe in more detail later in this chapter (also see appendix D).

## INDIVIDUAL COUGAR LOCATIONS

Of the 163 cougars we radio-collared during our two study phases, we limited spatial-habitat analyses to adult cougars originally captured and marked within Yellowstone National Park to ensure, to the degree possible, similarity in geographic extent between the two study periods. Over the PW study years 1987 through 1994, we collected 2,551 VHF telemetry locations on the eight females and six male cougars. Later, during the wolf restoration study in 1998 through 2005, we collected 2,866 VHF locations on twelve adult females and five adult males. On average we obtained 182 VHF locations (range = 50 to 371) over a period of 42.5 months (range = 14 to 77) on each adult in the PW study and 160 VHF locations (range = 37 to 377) over a period of 43.6 months (range = 19 to 87) on each adult cougar during wolf presence. To account for our error in estimating cougar locations, we chose a 250-meter-radius buffer around each point—the upper 95 percent confidence interval of PW aerial locations (Dickson and Beier 2002; Ruth et al. 2011). This also served the purpose of encompassing any errors inherent in the digital data we used on topography, cover type, elk use, and wolf use.

GPS technology acceptable for use on cougars was not yet available during much of the PW study, and only 2.4 percent of VHF locations were collected in the evening and at night. Similarly, 1.8 percent of VHF locations collected during the wolf restoration study were collected during the evening and at night. As a result, we felt grouping locations into day (morning and afternoon locations) and night (evening and night locations) periods was appropriate [1]. This meant that we necessarily limited inferences to daytime VHF locations in our comparison of spatial-habitat use of cougars during the PW and DW restoration study periods. Using our GPS data for the DW phase, we later tested whether cougars did indeed use resources differently during the day than during their nighttime movements, and we present the analysis later in this chapter. The following sections describe the subsets of these location databases used in our second- and third-order selection analyses.

## DEVELOPMENT OF HABITAT MODELS

We developed a suite of *a priori* models in three categories for males and females separately. The three categories represented: (1) intraspecific interactions between cougars and interspecific interactions between cougars and wolves and between cougars and prey, (2) static and temporally varying landscape attributes, and (3) combinations of species interactions and static and temporally varying landscape attributes. Because use of space could differ dramatically between sexes, with males covering much larger areas than females, we hypothesized that use of space by males would be influenced by habitat characteristics such as the distribution of steep terrain, access to food, locations of female cougars with the potential to be sexually receptive, and human access via roads (which influenced male mortality because of hunting outside the park). We hypothesized that use of space by females would be influenced by forested and rocky terrain that enabled access to food and provided security for offspring and by avoidance of areas frequented by wolves.

Based in part on previous exploratory analyses (see Ruth et al. 2003), we used environmental and resource variables hypothesized to influence cougar spatial use, including five variables related to topography, three variables related to forest cover, the amount of snow during winter, and locations where wolves and elk tend to spend time (table 11.1, appendix E). Three of our predictor variables for modeling summer and winter space use—wolf use, elk use, and amount

**TABLE 11.1.** Predictions (P) resulting from the hypothesis that variation in cougar space use and differences in landscape use of cougars and wolves are influenced by elk habitat use, competitor wolf use of the landscape, snow severity, characteristics of the landscape, and availability of female cougars in male home ranges. See appendix E for descriptions of data.

| <i>Independent Variable</i>                  | <i>Rationale and Predictions</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    | <i>References</i>                                                                                                                                            |
|----------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Wolf use                                     | <p>Because wolves are dominant competitors, cougars avoid wolves. During winter, cougars are less able to spatially avoid wolves than during summer because both carnivores are overlapped on elk winter range.</p> <p>P1: As wolf use increases, the probability of use by cougars decreases.</p> <p>P2: Cougars more strongly avoid areas frequented by wolves during summer compared to winter.</p> <p>P3: There is individual variation in cougar response to wolf use because wolf use varies across cougar home ranges.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   | Ruth 2004; Alexander et al. 2006                                                                                                                             |
| Elk use                                      | <p>Cougar home ranges are influenced by prey abundance and also by the distribution of prey through time, especially when a particular prey is a primary food source. Wolves select areas with high elk densities in the Western United States. In avoiding wolves, cougars are relegated to areas of lower elk use.</p> <p>P1: The probability of use in cougar home ranges decreases with increasing density of elk.</p> <p>P2: The magnitude of use is less in winter during wolf presence than prior to wolves in winter because wolves monopolize areas used by elk. The magnitude of use in summer is similar prior to and during wolf presence because elk are more dispersed on the landscape, use higher elevations, and use less open habitat.</p>                                                                                                                                                                                                                                                                                                                                                        | Sandell 1989; Durant 1998; Grigione et al. 2002; Mao et al. 2005; Oakleaf et al. 2006; Kauffman et al. 2007                                                  |
| Snow water equivalent                        | <p>In North America snow pack reports as an important factor affecting vulnerability of ungulate prey to wolves, but few studies have evaluated this predictor relative to cougar predation or in the context of avoidance of competitors. We expected that using areas of less snow would benefit cougars for hunting of prey and avoidance of wolves. The longer legs of wolves and their ability to travel through snow as a pack enhance their use of areas with greater snow depth relative to cougars.</p> <p>P1: Cougars select areas of low snow depth within their winter home ranges.</p> <p>P2: In avoiding wolves, the magnitude of use of areas with less snow is greater after wolf restoration compared to the pre-wolf period.</p>                                                                                                                                                                                                                                                                                                                                                                  | Kunkel et al. 1999; Mech and Peterson 2003; Gower et al. 2009b; Garrett et al. 2009b                                                                         |
| Edge density                                 | <p>Edges between forest and open habitat provide necessary structural components (cover) for successful hunting by cougars compared to strictly forest or nonforested habitats. Deer used edge and forest areas almost equally, but cougars killed more deer in edge habitat. Wolves also travel along hard edges because structural changes impede movements of prey, and elk were more vulnerable to predation by wolves when they were close to edges.</p> <p>P1: The probability of use in cougar home ranges increases with increasing edge density for cougars prior to and during wolf restoration.</p> <p>P2: In avoiding wolves, the magnitude of use is less after wolf restoration.</p>                                                                                                                                                                                                                                                                                                                                                                                                                  | Altendorf et al. 2001; Laundré and Hernández 2003; Bergman et al. 2006; Holmes and Laundré 2006                                                              |
| Elevation                                    | <p>Cougars and wolves migrate up and down in elevation following prey such as elk, deer, and moose that spend the summer in high-elevation areas and then migrate to valleys for the winter. During summer, elk migrate to higher elevations and are more dispersed on the landscape than during winter. Wolves are centralized at denning and rendezvous sites in summer; thus cougars should be able to spatially separate from wolves at higher elevations.</p> <p>P1: Cougars select lower elevations within their winter home ranges similarly prior to and during wolf presence.</p> <p>P2: Cougars select higher elevations within their home ranges during summer. The magnitude of higher-elevation use is greater after wolf restoration.</p>                                                                                                                                                                                                                                                                                                                                                             | Ballard et al. 1987; Ream et al. 1991; Pierce et al. 1999; Ruth 2004; Alexander et al. 2006                                                                  |
| Forest cover and topographic roughness index | <p>Wolves historically inhabited the prairie ecoregions and cougars the Montane and Intermountain ecoregions of Montana. Forest cover and topographically complex terrain enhance concealment of cougar kills from competitors compared to open habitats and provide a mixture of hunting and safety benefits to cougars, especially to females with kittens; these habitats support the highest densities of cougars. Cougars are averse to crossing or otherwise using flat open areas. At the second-order selection (landscape), wolves also select for forest cover but typically select for open habitats with relatively low topographic complexity within home ranges. Wolves have a more stable affinity for low elevation and less rugged valleys and plateaus during most times of the year.</p> <p>P1: The probability of use in cougar home ranges increases with increasing amount of forest and rough terrain for cougars prior to and during wolf restoration.</p> <p>P2: The magnitude of cougar use of forested and rough terrain within their home ranges is greater after wolf restoration.</p> | Logan and Irwin 1985; Laing and Lindzey 1991; Riley and Malecki 2001; Riley et al. 2004; Alexander et al. 2006; Holmes and Laundré 2006; Oakleaf et al. 2006 |

*continued on next page*

TABLE 11.1—continued

| <i>Independent Variable</i> | <i>Rationale and Predictions</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                | <i>References</i>                                                          |
|-----------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------|
| Distance to escape cover    | Cougars should remain close to forested and topographically complex habitat that provides security from competitors.<br>P1: The probability of use in cougar home ranges decreases as distance from escape increases for cougars prior to and during wolf restoration.<br>P2: The magnitude of use is greater after wolf restoration.                                                                                                                                                                                                                                                                                                                                           | Murphy 1998                                                                |
| Road density                | Although roads are few on the Greater Yellowstone Northern Range, they have a negative influence on wolf and cougar occupancy of the larger landscape and typically negatively influence cougar and wolf survival. Although we did not expect cougars to differ in their selection for or against roads between study phases, road density during the hunting season was a strong predictor of cougar survival; thus we included it in our habitat analyses. On the Greater Yellowstone Northern Range, we expected that wolves would be more likely to travel along roads, particularly during winter, than cougars.<br>P1: Cougars will avoid roads during both study phases. | Murphy 1983;<br>Mech et al. 1988;<br>Wydeven et al. 2001; Ruth et al. 2011 |
| Female cougar density       | A male cougar requires access to food for survival, but his reproductive success is ultimately determined by the availability of resident females and competition with other males.<br>P1: The probability of use by male cougars within their home ranges increases with the availability of females (female use).                                                                                                                                                                                                                                                                                                                                                             | Logan and Sweanor 2001, 2010                                               |

of snow on the landscape—changed dramatically over each season. We allowed for fluctuation in these variables by calculating averages over two-week periods (appendix E). This approach enabled us to assign each cougar location a value for wolf use, elk use, and snow cover associated with the specific time we recorded the location in the field. We developed models for summer (May–October) and winter (November–April) because the availability of certain resources, as well as the distribution and density of competitors, differed from summer to winter.

We created ecologically meaningful candidate models representing the processes described. In the end we compared a total of forty candidate models for both the second-order and third-order selection analyses. Prior to analysis, we tested variables for multicollinearity using Pearson's  $r$  (Hosmer and Lemshow 2000). We did not include highly correlated variables ( $r > 0.50$ ) in the same model [2].

## RESOURCE USE WITHIN THE STUDY AREA

The number of locations we obtained on each cougar varied across time frames, resulting in uneven sampling intervals across individual cats. For example, there were times when we obtained a location each day on some cats and only one per week on others. To maintain a consistent sampling interval between study periods, we randomly selected one location per week per cougar, the average aerial relocation inter-

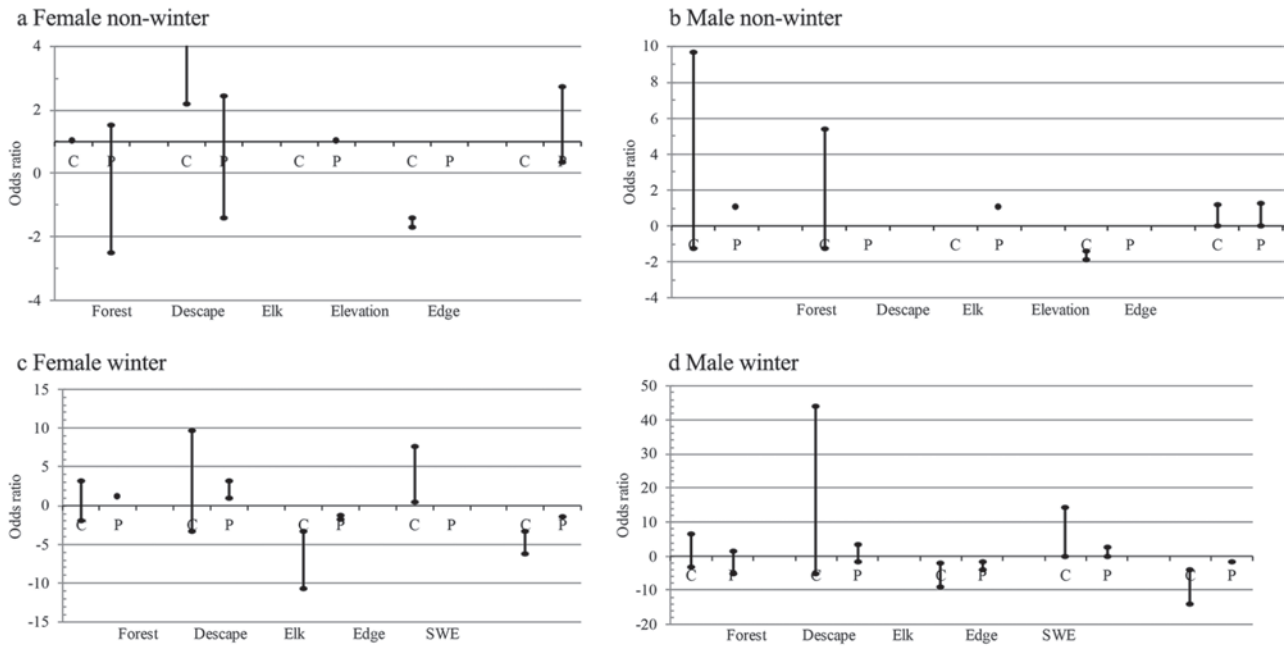
val across both study periods. We used 946 locations from eight adult females and 474 locations from six adult males prior to wolf presence and 1,591 locations from twelve adult females and 459 locations from five adult males during wolf restoration. We used Akaike's Information Criterion (AIC) to determine which logistic regression models best explained patterns of resource use across the study area (appendix D).

Overall, seasonal comparisons at the scale of the study area revealed that when living with their main competitor, both genders of cougars generally placed their home ranges in more secure habitats with lower availability of their primary prey—elk—particularly during winter, compared to cougars living without their main competitor. Exceptions to these patterns, which were also contrary to our predictions and which we discuss later, were: (1) that DW female home ranges included more areas farther from escape terrain, and (2) in summer, DW male home ranges were less topographically complex and rough compared to those of their PW counterparts.

## Winter

On the Greater Yellowstone Northern Range, snow accumulations throughout winter push elk to lower-elevation winter range (Houston 1982). Hence elk, wolves, and cougars overlapped on winter range. Snowpack was an important factor affecting vulnerability of ungulate prey to wolves, but to our knowledge, few studies have evaluated this predictor





**FIGURE 11.1.** Cougar resource use within the study area (second-order selection) during wolf presence relative to resource use of cougars prior to wolves. Odds ratio values above one indicate a greater probability of use, and odds ratio values below one indicate a lower probability of use. For example, in (d), cougars were roughly two times less likely to use areas with 13–18 centimeters (5–7 inches) of snow depth compared to areas with no snow (common on south-facing slopes and forested areas at lower elevations along the Black Canyon of the Yellowstone). Cougar resource use in core (C) and peripheral (P) areas within the study area (second-order selection) during wolf presence relative to their resource use prior to wolves.

relative to cougar predation or in the context of avoidance of competitors (Kunkel 1997; Mech and Peterson 2003; Atwood et al. 2009; Garrott et al. 2009a; Gower et al. 2009b). As we predicted, DW cougar home ranges were situated in areas of less snow than were PW cougar home ranges (fig. 11.1a, 11.1b). Also as we predicted, DW cougar home ranges encompassed areas of lower elk use compared to PW cougar home ranges. These differences were most noticeable in the core area of cougar ranges (figs. 11.1c, 11.1d, 11.2). If cougars were using more secure habitats to avoid wolves during winter, then they may have been relegated to areas of lower prey use within their winter home ranges. In addition, larger elk groups and their use of more open areas potentially inhibited access to prey by cougars. After wolf restoration, elk group sizes increased in areas of higher wolf density, and on a week-to-week basis elk did not avoid wolves during winter but used grouping—typically in more open areas—as an anti-predation strategy (Mao et al. 2005).

Bars indicate odds and 95 percent confidence intervals. Variables shown were included in top logistic regression models ( $\Delta\text{AIC} \leq 2.0$ ). For consistency of scale, the upper 95 percent confidence interval odds value of 37.1 for roughness for female summer in (c) and the lower 95 percent CI of -166.4 for roughness for male summer in (d) are not shown. Variable interpretation is as follows: forest is relative to in versus out of forest, distance to escape is relative to a 100 meter increase in distance from escape, roughness is relative to an increase equal to the maximum used, elk use is relative to an increase equal to the upper 95 percent CI of the mean used, elevation is relative to a 100 meter increase in elevation, and snow water equivalent is relative to a 2.54 centimeter increase (equaling 13–18 cm) in snow depth.

Bars indicate odds and 95 percent confidence intervals; C = 50 percent fixed kernel; P = 51–95 percent fixed kernel. Variables shown were included in top logistic regression models ( $\Delta\text{AIC} \leq 2.0$ ). For consistency of scale, the upper

95 percent CI odds value of 85.5 for distance to escape for female core in (a) is not shown. Variable interpretation is as follows: forest is relative to in versus out of forest, distance to escape is relative to a 100 m increase in distance from escape, roughness is relative to an increase equal to the maximum used, elk use is relative to an increase equal to the upper 95 percent CI of the mean used, elevation is relative to a 100 m increase in elevation, and snow water equivalent is relative to a 2.54 cm increase (equaling 13–18 cm) in snow depth.

During wolf restoration, core areas of both sexes included more edge habitat than did core areas of PW cougars. This, coupled with the lower use by elk within cougar core areas, indicated that when cougars were highly overlapped with wolves in winter, they apparently used edge habitats to hunt in the more secure part of their home range (fig. 11.1c, 11.1d). The border between forest and open zones provided stalking cover that probably increased a cougar's success at catching prey, which may be more important than just general prey abundance (Belden and Hagedorn 1993; Laundré and Hernández 2003; Bergman et al. 2006; Laundré and Loxterman 2007). During wolf cougars ventured farther

away from escape terrain and edge habitat to access and consume prey in the periphery of their home range, possibly reflecting their feeding on large prey, which were typically killed farther from escape cover. Although these analyses reflected times when cougars were less likely to be hunting, we found no difference between day and night habitat preferences, as we discuss later.

Contrary to our predictions, DW female cougar home ranges included more areas distant from escape terrain, particularly in the periphery of their winter home range, compared to PW female home ranges (figs. 11.1a, 11.1c, 11.3). Interpretations of the topographic complexity of female home ranges were less clear, but DW female home ranges tended to contain more topographically complex areas than their PW counterparts (table 11.2). The differing results for roughness and distance to escape may indicate variation in how individual cougars view security, with some preferring to remain in rough terrain for security while others were secure when simply close to rough terrain or tree cover. Furthermore, our definition of distance to escape terrain may not have reflected perfectly how cougars viewed such terrain. We chose a roughness level where higher roughness indicated escape terrain. It may be that cougars viewed roughness levels below this cutoff as escape terrain as well.



**FIGURE 11.2.** *Elk that grouped in open areas were probably better able to detect predators and reduce risk of predation; those shown were near Hellroaring Creek. Cougar core areas—especially of females—during wolf presence consisted of a greater degree of rugged terrain, with less snow, and were used by elk to a lesser degree than the core areas of cougars prior to wolf presence.*

## Summer

As wolves were restored, DW female cougars situated their summer home ranges in secure habitat—particularly rough terrain—to a greater degree than did PW females (fig. 11.1a). The difference was most noticeable in the periphery (outer 51–95 percent) of the home range, where there was also greater overlap with wolves (table 11.2, fig. 11.4). Similar to the situation in winter, DW female home ranges included areas more distant from escape terrain compared to those of PW females, but the greater distance from escape terrain was mostly associated with their core area (fig. 11.1a). Recall from chapter 10 that in both summer and winter, core areas of cougars were situated away from core areas of wolves, resulting in greater overlap of cougar and wolf periphery areas than core areas. In areas where the probability of encounters with wolves was greater and where rough terrain was typically more interspersed with the open grasslands on the Northern Range, DW female cougars selected for rough terrain more than did PW females. They could venture farther from escape cover while in their core area, as this part of



**FIGURE 11.3.** *Within the periphery of their winter home range, which overlapped with wolves more than did their core area, female cougars ventured farther from escape cover, sometimes to hunt low-density elk, while males remained in rugged terrain more than did their pre-wolf counterparts.*

their home range was already situated in secure habitat with lower probability of encounter with wolves.

In contrast to female cougars, DW male cougars situated their summer home ranges in less complex terrain than did their PW counterparts. During wolf restoration, the odds that home ranges of males included complex and rough terrain were 2 to 166 times less than prior to wolf presence (fig. 11.1d). In particular, PW male cougars oriented toward a much greater amount of rough terrain within their core area than did DW males (table 11.2, fig. 11.5). These results suggested to us that prior to wolves, male cougars were utilizing areas that provided access to prey while enhancing security from competitors, principally other male cougars.

In summer, elk migrated from lower to higher elevations (Skinner 1925; White et al. 2010). As wolves were restored on the Northern Range, DW elk selected for higher summer elevations than did PW elk, and they chose areas of lower wolf density during summer than winter (Mao et al. 2005). As a consequence, we expected that cougars would be able to access elk and avoid wolves by moving to higher elevations in summer. Instead, DW cougar home ranges, especially their core areas, were situated at lower elevations than those of PW cougars (fig. 11.1). Two explanations seem possible. First, enough prey may have remained at lower elevations that cougars did not need to shift to higher elevations. Second, cougars were simply constrained to lower elevations because of wolf activity. In either case, in addition to being



**FIGURE 11.4.** *Within the periphery of their summer home range, which overlapped with wolves more than did their core area, female cougars used a greater amount of edge and males remained in rugged terrain more than did their pre-wolf counterparts.*

located away from wolf core areas, core areas of DW cougars were situated in secure habitat that provided ample cover for hunting and escape.

Collectively, the data thus far support predictions that DW cougars generally situated their home ranges in more secure habitats with lower availability of their primary prey—elk—suggesting avoidance of wolves. This avoidance was particularly noticeable during winter. But how were cougars selecting resources within their home ranges, and was there clearer evidence that they avoided wolves?

## RESOURCE USE WITHIN HOME RANGES

To determine resource use within home ranges using the synoptic model approach, we used a single multi-year range for each cougar but split by season, so that all cougars had equal weight over a seasonal PW and DW time period (Creel and Creel 2002). We use the term *multi-year* to indicate a



**TABLE 11.2.** Cougar use of rough terrain during wolf presence compared to use before wolf presence: odds and lower and upper 95 percent confidence intervals (LCI, UCI) for cougar females and males (F, M).

| Odds Ratio | F Summer Core | F Summer Periphery | F Winter Core | F Winter Periphery | M Summer Core | M Summer Periphery | M Winter Core | M Winter Periphery |
|------------|---------------|--------------------|---------------|--------------------|---------------|--------------------|---------------|--------------------|
| LCI        | 0.7           | 34.7               | 0.2           | 0.9                | -2.8          | 0.0                | na            | 0.0                |
| Mean       | 5.3           | 348.1              | 4.2           | 11.9               | -62.8         | 0.5                | na            | 0.4                |
| UCI        | 39.1          | 3,495.6            | 95.0          | 154.7              | -1,405.7      | 24.5               | na            | 23.7               |

**FIGURE 11.5.** Within their summer core areas, cougars ventured farther from hunting and escape cover than did cougars prior to wolf presence. Male cougars used rugged terrain less than did their pre-wolf counterparts, but their home ranges were already situated in highly rugged areas on the Greater Yellowstone Northern Range.

home range using data pooled across more than one year of observation; thus a multi-year winter home range included locations across all winters for a particular animal (Dickson and Beier 2002). Although pooling data into multi-year winter and summer location data sets limited assessment of annual variation and may obscure important ecological patterns across months (Alexander et al. 2006), we felt that using information over a longer time frame strengthened

inferences about what factors influenced space use by cougars before and during wolf presence. In addition, we had less biological information on individual cougars during early and later years of each study phase, which would have limited the years and number of individuals for which we could assess spatial-temporal changes during the study. To ensure that locations were spatially independent, enabling us to make reliable comparisons between individuals, we



limited individual ground locations to every third day, as in our home range analyses.

We compared two underlying spatial, or null, models in the synoptic environment: the exponential power and the bivariate normal home range models (Jennrich and Turner 1969; Robledo-Arnuncio and Gil 2005; cited in Horne and Garton 2006a). The bivariate normal represented the possibility that cougars might use primarily two central areas of activity, with more localized movements around those centers (Horne and Garton 2006a). The exponential power model represented territorial behavior (Grant 1968; Covich 1976; cited in Horne and Garton 2006a). Because the spatial extent of each cougar might be better defined by one null model over the other, we compared model sets using each of the null models and then ranked the models using Akaike's Information Criterion (AIC, Akaike 1973; Burnham and Anderson 2002). The null models varied by individual, season, and study phase (table 11.3).

We developed synoptic models for each individual cat and defined our top model set using Akaike weights, as described in detail in appendix D. Because the strength and direction of the *beta estimate* for each variable varied across cougars, we weighted individual beta estimates by their associated standard errors when calculating population-level beta estimates for male and female cougars (see appendix D).

Before and during wolf restoration, cougars selected similar types of habitat within their home ranges [3]. During both study phases and seasons, forested and topographically rough areas and areas near escape and hunting cover were strong predictors of space use by male and female cougars (tables 11.4 and 11.5). Further, forested and rough terrain, snow depth, and wolf use during wolf restoration had greater importance for cougars selecting habitats relative to other landscape variables we considered (see variable importance, fig. 11.6). Cougars selected for rough terrain up to a limit; they did not use extreme topography (index values above 0.80) that reflected sheer cliffs, a finding similar to that for cougars in Arizona (Arundel et al. 2007).

Although cougars selected similar types of habitat, we did detect distinct changes in the *magnitude*, or strength, of certain beta estimates, indicating strong differences in certain habitats that cougars selected across the two study periods. To deduce the magnitude of the effect of each landscape variable on space use by each study population, we con-

**TABLE 11.3.** Distribution of top null spatial models for estimating utilization distribution within the synoptic model environment for female and male cougars by study phase and season before and during wolf restoration on the Greater Yellowstone Northern Range. Pre-wolf = 1987–94; during wolf = 1998–2006.

| <i>Study Phase and Season</i> | <i>Females</i>            | <i>Males</i> |
|-------------------------------|---------------------------|--------------|
| PRE-WOLF RESTORATION          |                           |              |
| Winter                        | 4 bvn, 4 exp <sup>a</sup> | 0 bvn, 6 exp |
| Summer                        | 3 bvn, 5 exp              | 1 bvn, 5 exp |
| DURING WOLF RESTORATION       |                           |              |
| Winter                        | 7 bvn, 5 exp              | 1 bvn, 4 exp |
| Summer                        | 3 bvn, 9 exp              | 1 bvn, 4 exp |

<sup>a</sup> Null spatial models compared were the bivariate normal home range model (bvn) and the exponential power model (exp); Jennrich and Turner 1969; Robledo-Arnuncio and Gil 2005; Horne and Garton 2006a).

verted weighted model-averaged beta estimates to probability ratios (see appendix F; Horne et al. 2008). We were then able to calculate the magnitude of differences of probability ratios for each season and gender and when comparing study phases. For example, during winter the probability ratios for PW male cougars and PW female cougars being in the roughest terrain compared to the least rough terrain were 11,985 and 493, respectively. Division of these two probability ratios equated to males being twenty-three times more likely to be in rough terrain than females.

## Winter

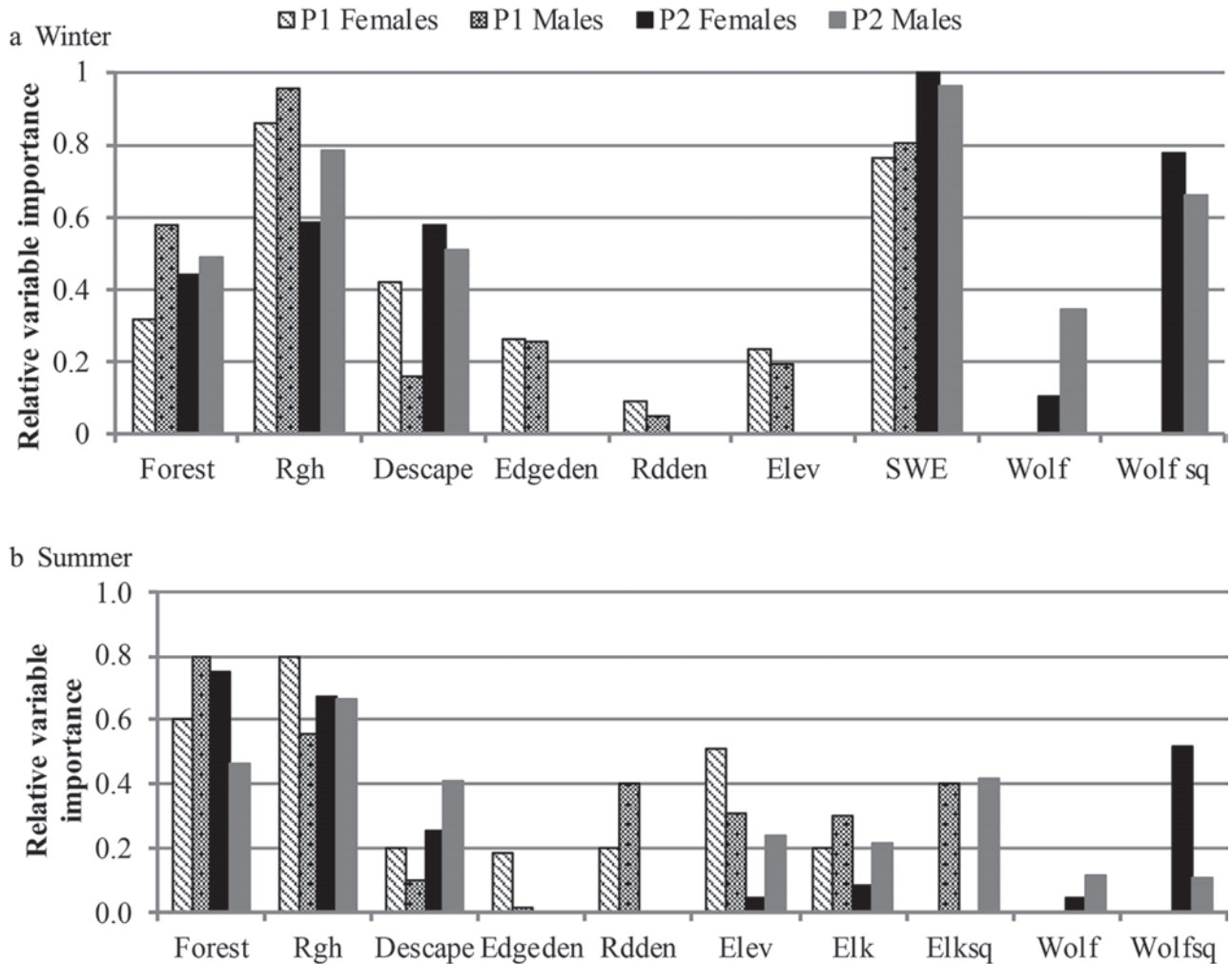
Forested and topographically rough areas, areas with less snow, at lower elevations, and near escape and hunting cover were strong predictors of space use within winter home ranges of cougars during both study phases (table 11.4, table 11.5, fig. 11.7). Although both sexes selected rough terrain much more often in winter than in summer, the preference was particularly apparent for adult males, which were thirty (PW) and sixty (DW) times more likely to be in rough terrain in winter compared to summer. In both study phases male cougars were twenty-four (PW) and two (DW) times more likely to be in rough terrain compared to females (table 11.6, fig. 11.7a). These results were consistent with research in Arizona and in Alberta, Canada, revealing that males selected terrain roughness more than did females and they did so more in winter than in summer (Arundel et al. 2007; Webb et al. 2011).

Despite the fact that male cougars placed their home ranges in similar amounts of rough terrain in the study area

**TABLE 11.4.** Examples of individual models used to estimate winter (November–April) utilization distribution of cougars before and during wolf presence on the Greater Yellowstone Northern Range, Wyoming and Montana.

| <i>Study Phase</i> | <i>Cougar ID</i>       | <i>Model<sup>a</sup></i>                          | <i>K</i> | <i>ΔAIC<sub>c</sub></i> | <i>w<sub>i</sub></i> |
|--------------------|------------------------|---------------------------------------------------|----------|-------------------------|----------------------|
| PRE-WOLF           | M2 ( <i>n</i> = 29)    | expp + forest + rgh + swe                         | 7        | 0                       | 0.68                 |
|                    |                        | expp + forest + rgh + swe + rd                    | 8        | 1.8                     | 0.28                 |
|                    | M8 ( <i>n</i> = 197)   | expp + forest + rgh + swe                         | 7        | 0                       | 1.00                 |
|                    |                        | expp + descaped + rgh + elev                      | 7        | 68.1                    | 0.00                 |
|                    | M28 ( <i>n</i> = 60)   | expp + edgeden + rgh + swe                        | 7        | 0                       | 0.88                 |
|                    |                        | expp + descaped + rgh + swe                       | 7        | 4.4                     | 0.10                 |
|                    |                        | expp + forest + rgh + swe                         | 7        | 7.2                     | 0.02                 |
|                    | F5 ( <i>n</i> = 169)   | expp + forest + rgh + elev                        | 7        | 0                       | 1.00                 |
|                    | F9 ( <i>n</i> = 122)   | bvn + forest + rgh + elev                         | 8        | 0                       | 0.74                 |
|                    |                        | bvn + descaped + rgh + elev                       | 8        | 2.1                     | 0.26                 |
|                    | F17 ( <i>n</i> = 71)   | bvn + descaped + rgh + swe                        | 8        | 0                       | 0.51                 |
|                    |                        | bvn + forest + rgh + swe                          | 8        | 0.4                     | 0.43                 |
|                    |                        | bvn + descaped + swe                              | 7        | 4.2                     | 0.06                 |
|                    | F48 ( <i>n</i> = 29)   | bvn + forest + rgh + swe                          | 8        | 0                       | 0.86                 |
|                    |                        | bvn + descaped + rgh + swe                        | 8        | 4.1                     | 0.11                 |
|                    | F53 ( <i>n</i> = 76)   | bvn + edgeden + rgh + swe                         | 8        | 0                       | 1.00                 |
|                    |                        | bvn + forest + rgh + swe                          | 8        | 12.8                    | 0.00                 |
| DURING WOLF        | M127 ( <i>n</i> = 54)  | expp + forest + rgh + wolf + wolfsq + swe         | 9        | 0                       | 0.40                 |
|                    |                        | expp + forest + rgh + rghsq + wolf + wolfsq + swe | 10       | 0.2                     | 0.36                 |
|                    |                        | expp + descaped + rgh + wolfsq + swe              | 8        | 3.0                     | 0.09                 |
|                    | M131 ( <i>n</i> = 37)  | bvn + descaped + rgh + swe + wolf                 | 9        | 0                       | 0.98                 |
|                    |                        | bvn + descaped + swe + wolf                       | 8        | 7.4                     | 0.02                 |
|                    | M137 ( <i>n</i> = 35)  | expp + forest + rgh + wolf + swe                  | 8        | 0                       | 0.17                 |
|                    |                        | expp + descaped + rgh + swe + wolf                | 8        | 0.4                     | 0.14                 |
|                    |                        | expp + forest + rgh + rghsq + wolf + wolfsq + swe | 10       | 0.4                     | 0.14                 |
|                    |                        | expp + descaped + rgh + wolfsq + swe              | 8        | 0.4                     | 0.14                 |
|                    |                        | expp + forest + rgh + rghsq + wolf + wolfsq       | 9        | 0.5                     | 0.13                 |
|                    |                        | expp + descaped + rghsq + wolfsq + swe            | 8        | 0.8                     | 0.11                 |
|                    |                        | expp + forest + rgh + wolf + wolfsq + swe         | 9        | 2.1                     | 0.06                 |
|                    | F47 ( <i>n</i> = 134)  | expp + descaped + rghsq + wolfsq + swe            | 8        | 0                       | 0.91                 |
|                    |                        | expp + forest + rgh + rghsq + wolf + wolfsq + swe | 10       | 5.9                     | 0.05                 |
|                    | F106 ( <i>n</i> = 82)  | expp + forest + rgh + wolf + wolfsq + swe         | 9        | 0                       | 0.58                 |
|                    |                        | expp + forest + rgh + rghsq + wolf + wolfsq + swe | 10       | 1.2                     | 0.31                 |
|                    |                        | expp + forest + rgh + wolf + swe                  | 8        | 4.8                     | 0.05                 |
|                    | F107 ( <i>n</i> = 103) | bvn + forest + rgh + rghsq + wolf + wolfsq + swe  | 11       | 0                       | 1.00                 |
|                    |                        | bvn + forest + rgh + wolf + wolfsq + swe          | 10       | 21.5                    | 0.00                 |
|                    | F123 ( <i>n</i> = 52)  | expp + descaped + rgh + swe                       | 7        | 0                       | 0.48                 |
|                    |                        | expp + descaped + rgh + swe + wolf                | 8        | 0.2                     | 0.43                 |
|                    |                        | expp + descaped + rgh + swe + wolfsq              | 8        | 4.5                     | 0.05                 |
|                    | F125 ( <i>n</i> = 78)  | bvn + descaped + rghsq + wolfsq + swe             | 9        | 0                       | 0.74                 |
|                    |                        | bvn + descaped + rgh + swe + wolf                 | 9        | 2.4                     | 0.22                 |

<sup>a</sup> Variables (described in greater detail in appendix E) are: bvn = bivariate normal space use model; expp = exponential power space use model; descaped = distance to nearest forest edge or rough terrain; forest = number of forested 30 meter cells within a 240 meter buffer; rgh = terrain roughness variable ranging from zero to two, with two the maximum topographical roughness possible and zero representing completely flat areas; rghsq = terrain roughness squared (quadratic term); edgeden = the hard boundary between forest and nonforest calculated in meters of edge per square meter of ground; elk = values of elk use based on elk resource selection functions (Mao et al. 2005); swe = snow water equivalent; wolf = index of wolf use based on locations and density of wolves; wolfsq = wolf use variable squared (quadratic term); afuse = index of adult female space use based on 95 percent utilization distribution grids.



**FIGURE 11.6.** Relative variable importance in cougar spatial and habitat use in winter (a) and summer (b) prior to wolf restoration (P<sub>1</sub>) and during wolf restoration (P<sub>2</sub>) on the Greater Yellowstone Northern Range, 1998–2005. Data from top third-order selection synoptic models; variable importance calculated as the sum of the Akaike weights from top models, including each particular variable divided by the sum of the full set of top model weights.

(second-order selection), male cougars did not orient as strongly toward rough terrain when wolves were present. Male cougars in the DW study were ten times *less* likely to be in rough terrain than their PW counterparts. As we highlight in several chapters, cougars in the PW study period may have been selecting habitats in response to competition from other male cougars, whereas DW male cougars were apparently less constrained in this regard because social structure and home ranges were more stable.

During both study phases, female cougars selected broadly similar habitats within their home ranges. However,

when female cougars were overlapped with wolves on winter range, they were more likely to be in or near habitat that provided security. Female cougars in the DW study were three times more likely to be in forested areas, two times more likely to be in rough terrain, and eight times more likely to be near escape terrain within their home ranges than were their PW counterparts (table 11.6, fig. 11.7a, 11.7b).

The degree to which cougars remained close to escape cover in winter varied little prior to wolf presence and varied widely when wolves were present. Prior to wolves, cougars were 2 to 5 times *less* likely to be 100 meters from escape

than to be in escape cover (table 13.6, fig. 11.7b). Once wolves were restored, both sexes of cougars were much less likely to venture far from cover, but this varied from 3 to 128 times less likely to be 100 meters from escape cover as they were to be in escape cover. This variation may be a reflection of the varying levels of overlap and competition with wolves and bears, as well as access to prey, that individual cougars experienced within their home ranges.

Along the river corridors, particularly at lower elevations and on south-facing slopes, there were many localized areas with low accumulations of snow or where snow was absent during much of winter (fig. 10.3). During both study periods, cougars selected these areas with less snow within their home ranges (table 11.6, fig. 11.7c). As wolves became established across the study area, male and female cougars had an even greater aversion to deep snow within their home ranges. During wolf males were 2 times less likely and DW females 1.5 times less likely to use areas with 12–16 centimeters of snow than to use areas with no snow compared to their PW counterparts. Because of their cursorial adapta-

tions, including long legs and webbed toes, and their single-file travel as a group, wolves were better able to negotiate the greater snow depths occurring at higher elevations and in more open terrain than were cougars (Mech and Boitani 2003a). Deep snow favored wolves after encounters with prey because it hindered ungulate locomotion (Huggard 1993; Post et al. 1999), and we found that wolves typically made kills in deeper snow and more open terrain than did cougars (see chapter 7). In addition to enabling cougars to travel and hunt more effectively, selecting areas with less snow may also better enable cougars to avoid risk of encounter and competition with wolves. As snow should hold scent for longer than bare ground, a lack of snow may also inhibit wolves' tracking ability.

As wolves were restored and their numbers and distribution increased across the study area, female cougars clearly avoided places that were increasingly used by wolves—probability of use declined as wolf use increased (table 11.6, fig. 11.7d). On average, female cougars were two times less likely to use areas frequented by wolves (average wolf use)

**TABLE 11.5.** Examples of individual models used to estimate the summer (May–October) utilization distribution of cougars before and during wolf presence on the Greater Yellowstone Northern Range, Wyoming and Montana.

| Study Phase | Cougar ID        | Model <sup>a</sup>                             | K  | $\Delta AIC_c$ | $w_i$ |
|-------------|------------------|------------------------------------------------|----|----------------|-------|
| PRE-WOLF    | M2 ( $n = 25$ )  | expp + forest + rgh + elk + elksq              | 8  | 0              | 0.57  |
|             |                  | expp + forest + rgh + rghsq + elk + elksq      | 9  | 1.3            | 0.29  |
|             |                  | expp + forest + rgh + elk + rd                 | 8  | 3.4            | 0.10  |
|             | M8 ( $n = 172$ ) | expp + forest + rgh + elk + rd                 | 8  | 0              | 0.46  |
|             |                  | expp + forest + rgh + rghsq + elk + elksq + rd | 10 | 0.1            | 0.44  |
|             |                  | expp + forest + rgh + elev                     | 7  | 4.6            | 0.05  |
|             | M28 ( $n = 78$ ) | bvn + forest + rgh + elk + rd                  | 9  | 0              | 0.90  |
|             |                  | bvn + forest + rgh + elev                      | 9  | 5.9            | 0.05  |
|             | F5 ( $n = 175$ ) | expp + descape + rgh + elev                    | 7  | 0              | 0.96  |
|             |                  | expp + forest + rgh + elev                     | 7  | 7.8            | 0.02  |
|             | F9 ( $n = 117$ ) | bvn + forest + rgh + elk + elev + rd           | 10 | 0              | 0.68  |
|             |                  | bvn + forest + rgh + elev                      | 8  | 2.6            | 0.19  |
|             |                  | bvn + descape + rgh + elev                     | 8  | 3.2            | 0.14  |
|             | F17 ( $n = 78$ ) | expp + forest + rgh + rghsq                    | 7  | 0              | 0.53  |
|             |                  | expp + forest + rgh                            | 6  | 2.3            | 0.17  |
|             |                  | expp + forest + rgh + elev                     | 7  | 2.9            | 0.12  |
|             | F53 ( $n = 41$ ) | bvn + forest + rgh + rghsq                     | 8  | 0              | 0.28  |
|             |                  | bvn + forest + rgh + elev                      | 8  | 0.3            | 0.25  |
|             |                  | bvn + forest + rgh                             | 7  | 2.1            | 0.10  |
|             |                  | bvn + forest + rgh + rghsq + elk + elksq       | 10 | 2.4            | 0.09  |

*continued on next page*



TABLE 11.5—continued

| Study Phase | Cougar ID      | Model <sup>a</sup>                                     | K  | $\Delta AIC_c$ | wi   |
|-------------|----------------|--------------------------------------------------------|----|----------------|------|
| DURING WOLF | M127 (n = 60)  | expp + descapse + rgh                                  | 6  | 0              | 0.11 |
|             |                | expp + forest + rgh                                    | 6  | 0.2            | 0.10 |
|             |                | expp + descapse + rgh + elk + elksq                    | 8  | 0.6            | 0.08 |
|             |                | expp + descapse + rgh + wolf                           | 7  | 0.9            | 0.07 |
|             |                | expp + forest + rgh + wolf                             | 7  | 1.2            | 0.06 |
|             |                | expp + descapse + rgh + elk                            | 7  | 1.4            | 0.06 |
|             |                | expp + forest + rgh + elk + elksq                      | 8  | 1.8            | 0.05 |
|             |                | expp + descapse + rgh + rghsq                          | 7  | 2.0            | 0.04 |
|             |                | expp + forest + rgh + elk                              | 7  | 2.0            | 0.04 |
|             |                | expp + descapse + rgh + elev                           | 7  | 2.0            | 0.04 |
|             | M131 (n = 40)  | expp + descapse + elk + elksq + wolf + wolfsq          | 9  | 0              | 0.21 |
|             |                | expp + descapse + elk + elksq                          | 7  | 0.7            | 0.15 |
|             |                | expp + descapse + elk                                  | 6  | 0.7            | 0.15 |
|             |                | expp + descapse + rgh + elk + elksq                    | 8  | 2.2            | 0.07 |
|             |                | expp + descapse + elk + wolf                           | 7  | 2.4            | 0.06 |
|             | M137 (n = 39)  | bvn + forest + rgh + elk                               | 8  | 0              | 0.18 |
|             |                | bvn + forest + rgh + elk + elksq                       | 9  | 1.5            | 0.09 |
|             |                | bvn + forest + rgh + wolf                              | 8  | 2.2            | 0.06 |
|             |                | bvn + forest + elk + elksq                             | 8  | 2.5            | 0.05 |
|             | F47 (n = 145)  | expp + forest + rgh + elk + elksq                      | 8  | 0              | 0.47 |
|             |                | expp + forest + rgh + rghsq + elk + elksq              | 9  | 0.2            | 0.43 |
|             |                | expp + forest + rgh + wolf + wolfsq + elk + elksq      | 10 | 3.5            | 0.08 |
|             | F106 (n = 91)  | expp + forest + rgh + wolf + wolfsq + elk + elksq      | 10 | 0              | 0.35 |
|             |                | expp + forest + rgh + elk + elksq                      | 8  | 0.2            | 0.31 |
|             |                | expp + forest + rgh + elk                              | 7  | 1.8            | 0.14 |
|             |                | expp + forest + rgh + rghsq + elk + elksq              | 9  | 2.3            | 0.11 |
|             | F107 (n = 121) | bvn + forest + rgh + wolf + wolfsq + elk + elksq       | 11 | 0              | 0.81 |
|             |                | bvn + descapse + rghsq + wolfsq + elksq                | 9  | 3.3            | 0.15 |
|             | F123 (n = 61)  | expp + forest + rgh + wolf + wolfsq + elk + elksq      | 10 | 0              | 0.71 |
|             |                | expp + descapse + rgh + wolf + wolfsq                  | 8  | 2.2            | 0.24 |
|             | F125 (n = 113) | bvn + elev + rgh + rghsq + elk + elksq + wolf + wolfsq | 12 | 0              | 0.94 |
|             |                | bvn + forest + rgh + elk + elksq                       | 9  | 7.1            | 0.03 |

<sup>a</sup> Variables (described in greater detail in appendix E) are: bvn = bivariate normal space use model; expp = exponential power space use model; descapse = distance to nearest forest edge or rough terrain; forest = number of forested 30 meter cells within a 240 meter buffer; rgh = terrain roughness variable ranging from zero to two, with two the maximum topographical roughness possible and zero representing completely flat areas; rghsq = terrain roughness squared (quadratic term); elk = values of elk use based on elk resource selection functions (Mao et al. 2005); wolf = index of wolf use based on locations and density of wolves; rdden = density of roads in kilometers of road/km<sup>2</sup>; elev = average elevation within a 240 meter buffer; afuse = index of adult female space use based on 95 percent utilization distribution grids.

compared to areas of no wolf use. Male cougars showed an even greater aversion to wolves—they were two to eight times less likely to be in areas used by wolves compared to areas of no wolf use (table 11.6, fig. 11.7d) [4].

Collectively, these responses supported our a priori prediction that cougars would manifest a strategy of seeking habitats that provided security from dominant competitors

and, as we elaborate later, that such a response should be greater in winter compared to summer.

### Summer

In summer, cougars also favored forested and rough terrain in both study phases, although not to the degree they did in winter (tables 11.5, 11.6). Similar to behavior in winter, DW

**TABLE 11.6.** Probability ratios (and 95 percent confidence intervals) for cougar use of landscape variables relative to availability within their home ranges. More likely = normal text; less likely = bold italics. Values indicating that cougars were less likely to use a certain landscape variable were calculated as 1/probability ratio. Probability ratios were developed from the weighted average population-level synoptic models with 90 percent model weights. Only variables that were common to both phases are shown, except for wolf use, which applied to the during wolf study only.

| Time Period and Landscape Variable <sup>a</sup> | Pre-Wolf    |                               |             |                                | During Wolf  |                      |            |                                  |
|-------------------------------------------------|-------------|-------------------------------|-------------|--------------------------------|--------------|----------------------|------------|----------------------------------|
|                                                 | Females     |                               | Males       |                                | Females      |                      | Males      |                                  |
| WINTER                                          |             |                               |             |                                |              |                      |            |                                  |
| Forest                                          | 3.8         | (1.1–13.1)                    | 4.3         | (2.5–7.2)                      | 10.9         | (3.5–33.3)           | 4.1        | (1.1–16.1)                       |
| Roughness                                       | 493.2       | (191.7–1,269.0)               | 11,985.1    | (1,155.7–124,284.8)            | 882.5        | (184.0–4,231.5)      | 1,924.9    | (226.7–16,340.7)                 |
| Distance to escape                              | <b>4.0</b>  | <b>(3.0–5.3)</b>              | <b>3.2</b>  | <b>(2.4–4.2)</b>               | <b>32.9</b>  | <b>(8.5–127.7)</b>   | <b>7.7</b> | <b>(2.8–20.7)</b>                |
| SWE <sup>b</sup>                                | <b>1.6</b>  | <b>(1.5–1.7)</b>              | <b>1.6</b>  | <b>(1.5–1.6)</b>               | <b>2.5</b>   | <b>(2.1–2.9)</b>     | <b>3.0</b> | <b>(2.2–4.1)</b>                 |
| Elevation                                       | <b>27.9</b> | <b>(9.6–80.8)</b>             | <b>75.3</b> | <b>(17.6–333.2)</b>            |              |                      |            |                                  |
| Wolf use                                        |             |                               |             |                                | <b>2.0</b>   | <b>(1.8–2.3)</b>     | <b>3.6</b> | <b>(1.6–8.1)</b>                 |
| SUMMER                                          |             |                               |             |                                |              |                      |            |                                  |
| Forest                                          | 4.2         | (2.6–6.8)                     | 3.2         | (1.6–6.3)                      | 5.1          | (4.0–6.6)            | 5.1        | (3.0–8.6)                        |
| Roughness                                       | 199.0       | (70.8–558.9)                  | 402.9       | (23.2–7,003.0)                 | 837.0        | (350.7–1,999.4)      | 31.8       | (7.5–134.1)                      |
| Distance to escape                              | <b>14.6</b> | <b>(2.5–85.7)</b>             | <b>3.6</b>  | <b>(0.8–15.0)</b>              | <b>3.6</b>   | <b>(1.6–8.1)</b>     | <b>2.3</b> | <b>(1.2–4.4)</b>                 |
| Elk use                                         | <b>3.1</b>  | <b>(0.3–32.5)<sup>c</sup></b> | <b>0.1</b>  | <b>(0.0–200.3)<sup>c</sup></b> | <b>122.6</b> | <b>(6.7–2,258.6)</b> | <b>3.7</b> | <b>(0.0–4,761.9)<sup>c</sup></b> |
| Elevation                                       | <b>3.2</b>  | <b>(4.6–2.1)</b>              | <b>4.7</b>  | <b>(2.7–8.0)</b>               | <b>1.8</b>   | <b>(1.4–2.3)</b>     | <b>2.8</b> | <b>(2.0–3.8)</b>                 |
| Wolf use                                        |             |                               |             |                                | 1.8          | (1.2–2.9)            | 1.6        | (1.1–2.1)                        |

<sup>a</sup> Cougars were more likely (normal text) or less likely (**bold italics**) to be: in forest compared to not forest, in the roughest terrain available compared to the least rough available, 100 meters from escape cover compared to in escape cover, in the maximum amount of elk use compared to no elk use, somewhere with 12–16 centimeters (5–7 inches) of snow compared to areas with no snow, 1 kilometer above the lowest elevation compared to at the lowest elevation, and in the upper 95 percent confidence interval of mean wolf use compared to no wolf use.

<sup>b</sup> SWE = snow water equivalent, defined in appendix E.

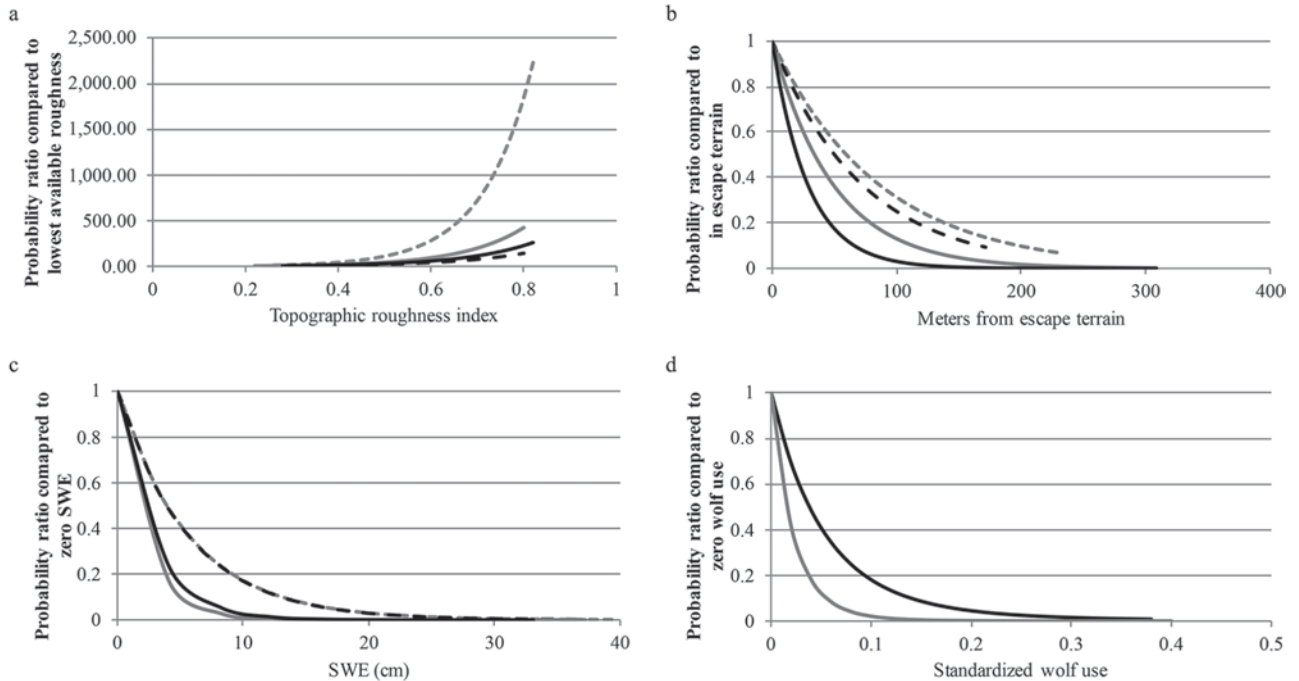
<sup>c</sup> The 95 percent confidence intervals overlapped 0 for pre-wolf female and male cougars and during wolf male cougars.

female cougars showed stronger selection for rough terrain (2 times greater) and DW males showed less selection for rough terrain (13 times less) within their summer home ranges than did PW female and male cougars (table 11.6, fig. 11.8a). In contrast to winter, DW cougars were more likely to be farther from escape terrain in summer compared to their PW counterparts (table 11.6, fig. 11.8b).

Compared to PW cougars, space use of DW female cougars decreased as elk use increased (table 11.6, fig. 11.8c). During wolf presence, female cougars were roughly forty times less likely to use areas frequented by elk (average elk use) within their summer home ranges compared to their PW counterparts. In general, male cougars during wolf presence used areas with lower values of elk use compared to their PW counterparts, but clear interpretation was difficult because of wide confidence intervals [5]. These findings, in combination with both genders venturing farther from escape terrain, suggested that cougars—particularly females—took greater risks when

hunting and consuming prey within their home ranges, which were situated within secure forested and rocky terrain in the study area. Compared to PW cougars, summer kills of DW cougars occurred in areas with lower elk use, in less rough terrain, and farther from escape terrain; and kills were less likely to be within the core area of cougars (see chapter 7). Perhaps cougars only try to access areas used more frequently by elk when they are actively hunting, which occurs most commonly at night, but we found no difference in cougar habitat use during the day compared to at night—a topic we address later.

Cougars did not consistently avoid wolves during summer to the degree they did in winter. Although cougars used areas where wolves were present—mostly areas with low frequency of use by wolves—they clearly did not use areas with the greatest use by wolves (fig. 11.8d). Both genders of cougars preferred areas with a similar amount of wolf use, yet their response to increasing wolf use differed. Male cougars exhibited a monotonic increase with increasing wolf



**FIGURE 11.7.** Probability of cougar use during daytime in winter (November–April, 0800–1600 hrs) across the range of used values for (a) topographic roughness, (b) meters from escape terrain, (c) snow water equivalent, and (d) wolf use. Probability of use in each graph is shown in dashed lines for pre-wolf cougars and solid lines for cougars during wolf restoration (female, black; male, gray). Probability ratio values above one indicate a greater probability of use, and values below one indicate a lower probability of use. For example, in (c), cougars were less likely to use areas of increasing snow depth compared to areas with no snow (common on south-facing slopes and forested areas at lower elevations along the Black Canyon of the Yellowstone).

use. Unlike males, females showed selection for intermediate ranges of wolf use while using lower and higher wolf use areas less (see fig. 11.8d, table 11.7, table 11.8). Female cougars may have used density and intensity of wolf use as information on resource quality and costs of competition, as we discuss later.

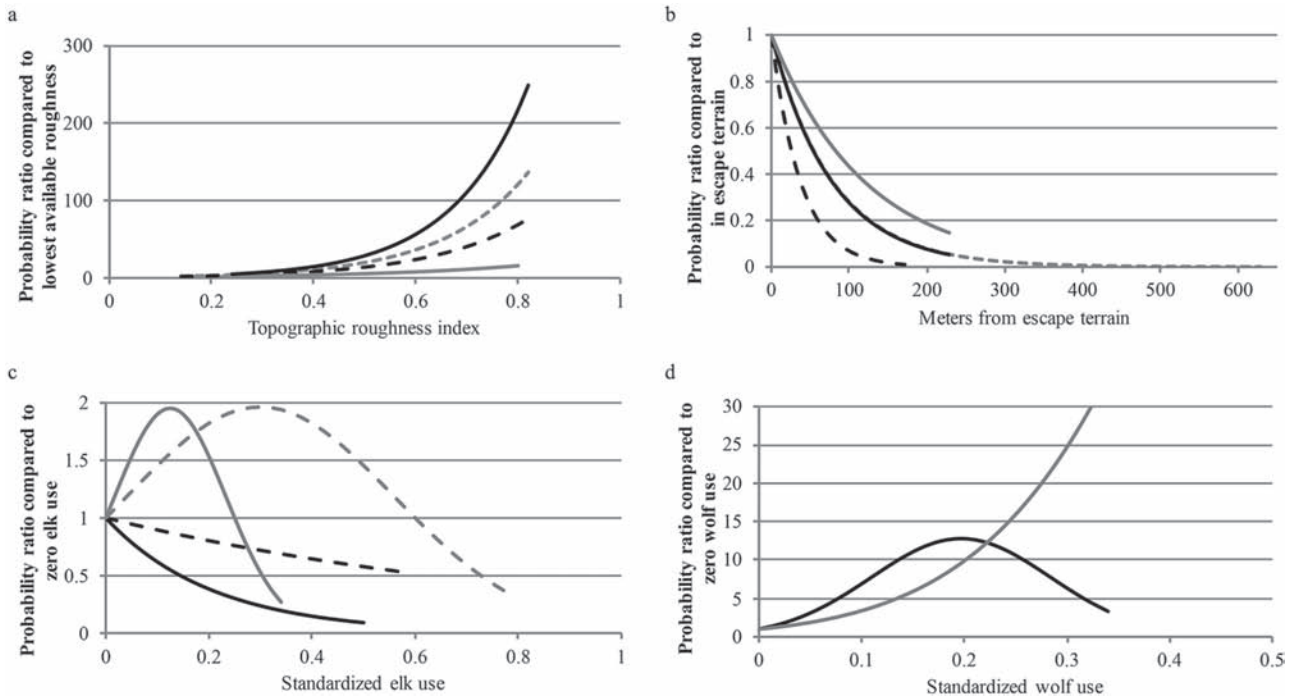
In summary, comparisons at the scale of the home range revealed some consistent patterns of selection between study periods but also some important differences in the magnitude of selection preferences. During both study periods cougars selected for forest cover and rough terrain. Despite this, as wolves were restored on the Greater Yellowstone Northern Range, cougars were even more likely to use forested and rough terrain, which held lower use by prey but was also little used by wolves. At this third-order population level, analysis revealed two seasonal patterns: within their winter home ranges, cougars strongly avoided areas used by wolves; during summer, most cougars preferred those areas within their home range that

were less frequently used by wolves (wolf use values less than 0.36).

The fine-scale habitat and topographic features within each home range strongly influenced cougar, wolf, and elk habitat selection, creating areas with variable levels of competition and predation risk (White et al. 2009c). Consequently, within the study area we expected that not all individual cougars experienced the same level of risk, responded similarly to risk, or sought out prey in the same manner. We examined this individual variation to gain a clearer picture of how DW cougars responded to wolves and elk within their home ranges.

### Individual Variation

As we found in chapter 10, some cats maintained home ranges that overlapped wolves very little, whereas the home ranges of others were completely subsumed within multiple wolf territories. Some cats simply appeared to live in the best



**FIGURE 11.8.** Probability of cougar use during daytime in the summer months (May–October, 0800–1800 hrs) across the range of used values for topographic roughness (a), meters from escape terrain (b), elk use (c), and wolf use (d). Probability of use in each graph is shown in dashed lines for pre-wolf cougars and solid lines for cougars during wolf restoration (female, black; male, gray). Probability ratio values above one indicate a greater probability of use, and values below one indicate a lower probability of use. For example, in (b), female and male cougars were less likely to be 100 meters from escape than to be in escape cover both prior to and during wolf restoration. The linear term for elk use was included in models for female cougars prior to wolf restoration, but it bounded zero and is shown in this graphic for comparison to female cougars (linear term for elk use) during wolf presence and male cougars (quadratic term for elk use) prior to and during wolf presence (shown in c).

cat habitat—rocky steep terrain that probably coincided with low use by wolves. Thus their home ranges were naturally situated in areas that were used less by wolves and that also provided superior escape and hunting cover.

As we expected, there was less variation in habitat selection by individual cougars in winter than in summer (fig. 11.9). Individuals avoided wolves more similarly during winter, with eleven of fourteen cougars strongly avoiding wolves—even those cougars living in areas wolves used infrequently (fig. 11.9a). In summer the pattern of response to wolf use varied by individual (fig. 11.9b). Even cougars that were highly overlapped with wolves did not all respond similarly—some strongly avoided wolves across low and higher intensities of wolf use, while others did not. For instance, two females with the greatest amount of overlap

with wolves, F106 and F125, responded quite differently to wolf use during summer. Female F106 avoided wolves at all levels of use, whereas F125 did not avoid wolves up to a point, after which she showed avoidance of areas with the highest wolf use (fig. 11.9b). Such differences in behavior among individuals probably arise from differences in their genes, their experience, and the characteristics of their home ranges, so it is not surprising that they may differ in how they respond to variation in access to resources or risk of competition (Tierney 1986; Riechert 2005). We delve into this concept and the importance of individual variation in the resiliency of the population in chapter 17.

Cougars also exhibited variation in their association with predicted elk use within their summer home range (fig. 11.10). At low values of elk use, seven of fourteen cats were more



**TABLE 11.7.** Top logistic regression models ( $\Delta AIC \leq 2.0$ ) of cougar landscape use relative to wolf landscape use on the Greater Yellowstone Northern Range, 1998–2005.

| <i>During Wolf</i> | <i>Models<sup>a</sup></i>                   | <i>df</i> | <i>AIC</i> | $\Delta AIC$ | <i>Model Weight</i> | <i>AUC<sup>b</sup></i> |
|--------------------|---------------------------------------------|-----------|------------|--------------|---------------------|------------------------|
| <b>SUMMER</b>      |                                             |           |            |              |                     |                        |
| Females            | forest + rghasp + elk                       | 4         | 1,556.06   | 0.0          | 0.79                | 0.86                   |
|                    | forst + rghasp + rghsq + elk + elksq        | 6         | 1,558.74   | 2.7          | 0.21                | 0.86                   |
|                    | descape + rghasp + elk                      | 4         | 1,584.73   | 28.7         | 0.00                | 0.85                   |
| Males              | forest + rghasp + elk                       | 4         | 704.35     | 0.0          | 0.85                | 0.83                   |
|                    | forst + rghasp + rghsq + elk + elksq        | 6         | 708.041    | 3.7          | 0.13                | 0.84                   |
| <b>WINTER</b>      |                                             |           |            |              |                     |                        |
| Females            | forest + rghasp + elk + swe                 | 5         | 2,038.33   | 0.0          | 0.92                | 0.87                   |
|                    | forest + rghasp + rghsq + elk + elksq + swe | 7         | 2,044.22   | 5.9          | 0.05                | 0.87                   |
| Males              | forest + rghasp + elk + swe                 | 5         | 736.62     | 0.0          | 0.99                | 0.87                   |
|                    | forest + rghasp + rghsq + elk + elksq + swe | 7         | 747.13     | 10.5         | 0.01                | 0.88                   |

<sup>a</sup> Variables (described in greater detail in appendix E) are: descape = distance to nearest forest edge or rough terrain; forest = number of forested 30 meter cells within a 240 meter buffer; rghasp = terrain roughness variable ranging from zero to two, with two the maximum topographical roughness possible and zero representing completely flat areas; rghsq = terrain roughness squared (quadratic term); elk = values of elk use based on elk resource selection functions (Mao et al. 2005); elksq = elk use squared (quadratic term); swe = snow water equivalent.

<sup>b</sup> AUC = Receiver operating characteristics area under the curve providing an assessment of model fit.

likely to use an area as elk use increased, but above a threshold (values of 0.3), use by most cats declined with increasing use by elk. In avoiding wolves most cougars were relegated to areas with lower elk use, as wolves dominated areas used more frequently by elk (fig. 11.11). Overall, elk did not change the way they used the landscape very much, although they did select for higher summer elevations during wolf restoration compared to before wolf presence, and they selected areas of lower wolf density during summer relative to winter (Mao et al. 2005; Kauffman et al. 2007).

### Did Space Use by Males Reflect Access to Females?

A male cougar requires access to food for survival, but because he can potentially inseminate many mates, his reproductive success is ultimately determined by the availability of resident females and the number of other males with which he competes (Emlen and Oring 1977; Clutton-Brock 1989; Logan and Sweaner 2001). Thus, in addition to access to prey, we might expect that by defending the ranges of several females, space use by males within their home ranges should also reflect access to females (Macdonald 1983). From chapter 10 it is apparent that during wolf restoration, home ranges of male cougars overlapped with those of four to six females by anywhere from 60 percent to 100

**TABLE 11.8.** Cougar use of rough terrain during wolf presence compared to wolf use of rough terrain: mean odds and lower and upper 95 percent confidence intervals (LCI, UCI) for cougar females and males (F, M). Odds are relative to an increase of the maximum roughness used.

| <i>Odds</i> | <i>F Summer</i> | <i>M Summer</i> | <i>F Winter</i> | <i>M Winter</i> |
|-------------|-----------------|-----------------|-----------------|-----------------|
| LCI         | 234459          | 344880          | 10877           | 54332           |
| Mean        | 1439778         | 1962815         | 166042          | 1252145         |
| UCI         | 8841437         | 11170946        | 2534635         | 28856846        |

percent. To ascertain whether availability of adult females helped explain variation in space use of adult males, we used location information from radio-collared adult females to include a covariate representing the spatial extent and availability of adult females. We had sufficient data for this analysis for three adult males prior to presence of wolves and three adult males during wolf restoration.

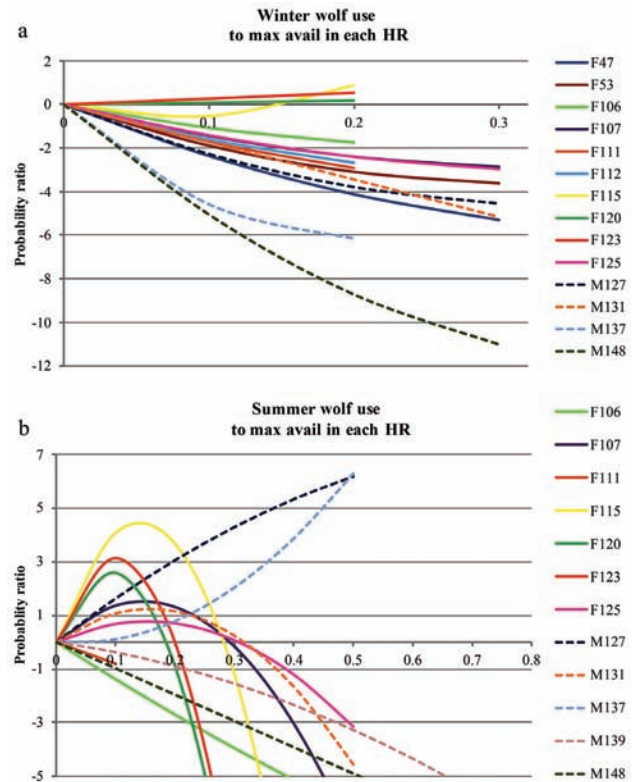
Adult female use was included in top seasonal models for two of three males during each of the two study phases, but it had little overall influence in any of the model sets. Hence, compared to forested and rough terrain, elk use, and snow depth, adult female use had little overall influence on use of space by males [6]. Although we limited data to years when we had the most females collared, the existing data may have been inadequate to capture the temporal availability of all females within a male's territory when looking at each study

phase. Our findings here do corroborate our home range regression findings in chapter 10. That is, within each study period, the sizes and orientation of the home ranges of males were most strongly related to prey and the density of female cougars. Over the longer time frame of both study periods, the home ranges of males exhibited a stronger relationship to the density of female cougars (see chapter 10). As a result of overlapping several females, males benefited from the same food resources as females because female home ranges were affected by the availability of prey (Seidensticker et al. 1973; Sandell 1989; Logan and Sweanor 2001).

### DID COUGARS USE SIMILAR HABITATS DURING NIGHTTIME MOVEMENTS?

On the Greater Yellowstone Northern Range, day bed sites probably represent the most secure habitats used by cougars and thus may limit interpretation of how cougars responded to wolf presence during periods of greater cougar activity. Our spatial habitat findings were necessarily limited to daytime locations for appropriate comparisons between the PW and DW study phases. Thus we expected that the types of habitats cougars used while traveling and hunting when wolves were also most active—at night—should yield differences compared to daytime, when wolves and cougars were less active. On one hand, cougars might take greater risks and venture farther from cover while hunting prey. Then again, to avoid wolves, cougars might remain near escape habitat during the night, as during the day.

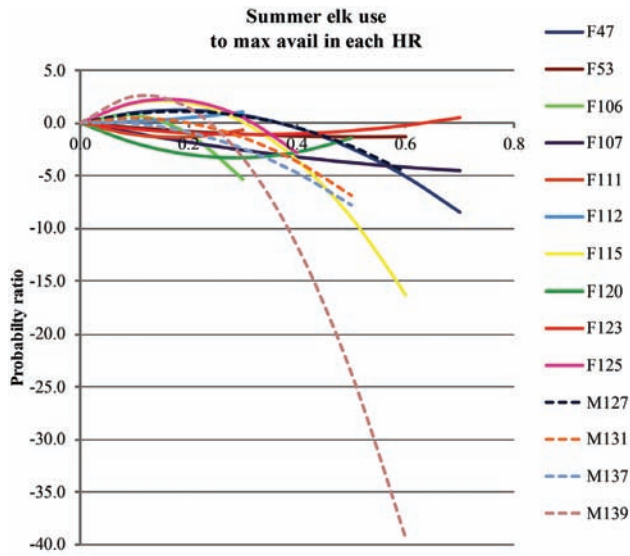
The use of GPS collars allowed us to sample cougar and wolf movements and habitat use through the day and night during the DW restoration study period. We used 4,807 GPS locations collected during the day and 5,494 GPS locations collected during the night on five adult female cougars during wolf restoration to evaluate if inferences from our daytime habitat analysis could be used to describe nighttime habitat use. For five adult males, we used 1,192 daytime GPS locations and 2,918 GPS locations collected at night. During the same years, we obtained 3,072 GPS locations on seven wolf packs using the Greater Yellowstone Northern Range. To achieve spatial independence, we constrained these data to one location every third day or night for cougars and one location per day or night per wolf pack. Because information on habitat use is best obtained by varying location time schedules so that all times of the day are sampled on multiple individuals during a year, our inferences of habitat use were



**FIGURE 11.9.** Variation in how individual cougars responded to wolf use within their home ranges during winter (a) and summer (b) across the range of values to the maximum wolf use in each individual cougar's home range. During winter, eleven of fourteen cats strongly avoided wolves, even at low values of wolf use. There was greater variation between individuals and a greater range of wolf use within home ranges during summer. One male cougar during winter and five females and one male cougar during summer are not shown because wolf use was not included in their top synoptic model set.

somewhat limited as a result of our fixed location schedule. Yet because radio-collared adult cougars represented a broad cross-section in sex and reproductive status, we assumed that the locations were representative of the population as a whole (Ciarniello et al. 2007).

Using these data, we first asked if cougars used habitats differently during their nighttime travels compared to during the day. We accomplished this with two methods: (1) comparing a priori models of night and day locations via logistic regression and ranking models with AIC and (2) running synoptic models with our night locations and comparing the data to the daytime synoptic model set. Next,

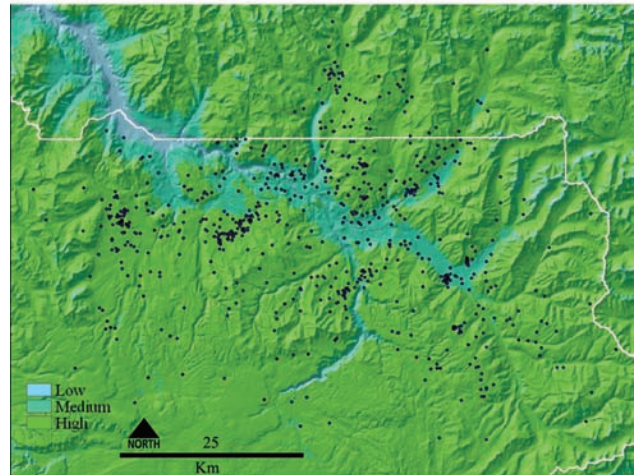


**FIGURE 11.10.** Variation in elk use during summer across the range of values to the maximum elk use in each individual cougar's home range. At low values of elk use ( $<0.3$  elk resource selection function, RSF, value), seven of fourteen cats were more likely to use areas of low elk use, but above that threshold all cats were less likely to use areas with greater elk use. As we discuss in the text, wolves were more likely to dominate areas of greater elk use. One male cougar is not shown because elk use was not included in his top synoptic model set.

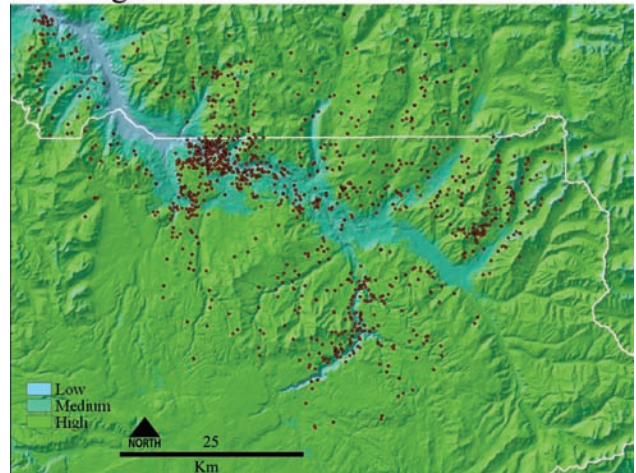
we questioned if there were greater separation in habitat use during nighttime movements of cougars and wolves and if these differed from the set of variables that explained variation in daytime habitat use between the two species (daytime cougar-wolf differences are described later). For this analysis we compared a priori models using night locations of cougars and night locations of wolves via logistic regression and ranked models with Akaike's information criterion, as previously described.

In all three comparisons we found poor model fit—such that it was like tossing a coin—for discriminating between night and day habitat use with logistic regression [7]. When comparing synoptic models for two female and two male cougars that were GPS-collared for the longest duration, we found no consistent patterns of differences across individuals, and there was very little difference within individuals in habitat use in home ranges during the day versus at night. Finally, cougars used habitat differently from wolves, but how they used habitat was consistent during day and night: cougars remained in or closer to forested and rough terrain

## a Wolves



## b Cougars



**FIGURE 11.11.** Summer locations of northern Yellowstone wolves (a, black points) and cougars (b, red points) plotted over low, medium, and high values of elk use during summer. Elk use is the average maximum elk use across the years of the study and based on the elk resource selection function (RSF; Mao et al. 2005; Kauffman et al. 2007). To classify features using natural breaks in data values, we used the Jenks optimization method, also known as the goodness of variance fit (GVF, <http://support.esri.com/en/knowledgebase/techarticles/detail/26442>, accessed September 28, 2011).

much more than did wolves in both seasons. During winter day and night, cougars avoided deep snows more than did wolves, but the two species were associated with similar values of elk use. The similarity in elk use did not hold during



summer, as during both the day and night, female cougars consistently used areas with lower elk use compared to areas used by wolves. Thus, during summer, wolves dominated areas with higher values of elk use, which was supported by our analyses that follow.

In our study area we found that during day and night, cougars rarely ventured far from escape cover—only 3.9 percent and 3.3 percent of GPS locations were greater than 100 meters from escape cover in winter and summer, respectively (fig. 11.12) [8]. We defined distance from escape terrain as meters from the closest of either forest or high roughness (defined as 1.1 in our topographic roughness layer; see appendix E). The greatest distances cats ventured from escape cover, 300 to 555 meters, occurred infrequently, with 59 percent (17 of 29 locations) of such excursions made by males in winter and 83 percent (10 of 12 locations) made by females in summer. These distances were substantially less than the distances of over 1,000 meters from cover observed for some Florida panthers (Onorato et al. 2011a: fig. 3, 202). In Florida and California, cougars used forests less and traversed open prairie grasslands more at night than during the day (Dickson et al. 2005; Onorato et al. 2011a). In these systems use of open areas such as grasslands apparently facilitated movements of cougars as they traveled and hunted for prey (Dickson et al. 2005; Onorato et al. 2011a). Given that movement rates of cougars on the Greater Yellowstone Northern Range were greater at night as they hunted and made kills, why did we not observe similar patterns of cougars traversing open meadows and using areas farther from escape cover?

We propose two hypotheses for why cougars did not use open areas but remained equally close to escape cover during the night as during the day and why our findings differ from those in Florida and California. First, the similarities we found may indicate that habitats frequented by cougars on the Greater Yellowstone Northern Range provide refuge similarly during both day and night in a wolf- and bear-dominated system. Cougar activity corresponds to the activity patterns and periods of vulnerable prey, and prey activity typically peaks in late afternoon and during crepuscular periods (Eberhardt et al. 1984; Kufeld et al. 1988; Green and Bear 1990; Beier et al. 1995). Wolves and cougars hunted similar prey, and wolves were most and least active at similar times to cougars: most active 1900–0900 hours, least active 1000–1700 hours. In summer, female

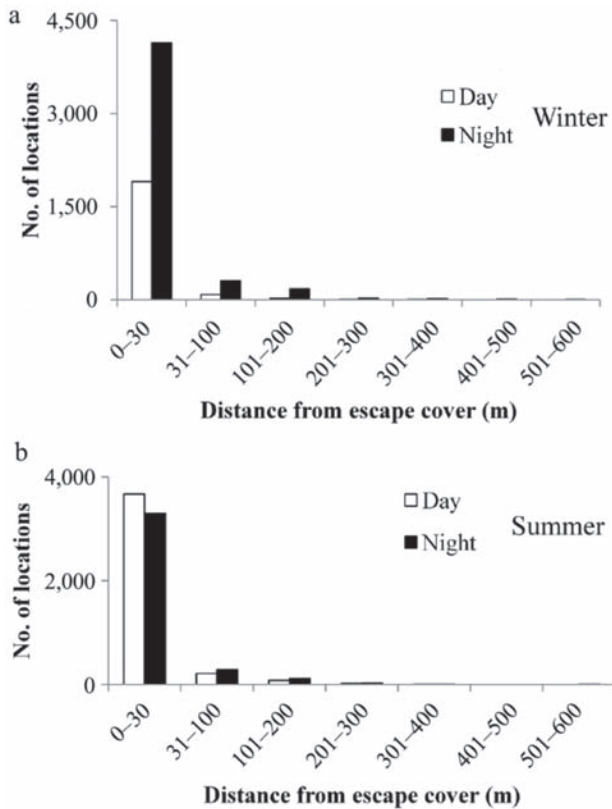
grizzly bears were least active between midnight and 0500 hours, and male bears were least active between 1000 and 1700 hours (Interagency Grizzly Bear Study Team, unpubl. data, 2005). By remaining close to escape cover, cougars may reduce encounters with both competitors. We found a similar pattern with subadult cougars that dispersed from our study area—they also used similar habitats during the day and at night (Newby 2011).

Second, in more human-dominated landscapes, cougars use habitat differently during day and night hours because (1) they avoid areas and times with high human activity, or (2) their natural behavior—day resting and night hunting—places them in certain habitats at times when people are not active (see Sweanor et al. 2008: 1082). Although cougars demonstrate great plasticity in their response to humans, they frequently show avoidance of areas with increased human use—roads, trails, recreational areas, hunting areas—and avoidance of times when humans are most active (Ruth 1991; Janis and Clark 2002; Ellingson 2003; Arundel et al. 2007; Sweanor et al. 2008). Although cougars are usually most active at dawn, dusk, and nighttime, they adjust their activity patterns within urban areas to be more active at night after human activity declines (Allredge 2011). Thus cougars are able to avoid humans and travel trails or open grasslands at night because humans are not active and other large competitors are less abundant—or largely absent—in Florida and California (Sweanor et al. 2008). During resting cougars are situated in areas of greater cover, which also provide refuge from human activity during the day. Although people use Yellowstone for recreation, their use of the Greater Yellowstone Northern Range distant from roads is expected to be much less than the human activity in the more human-dominated landscapes of Florida and California. Another possibility is that cougars use habitats similarly in more temperate climates because they do not need to find respite from the extreme temperatures and humidity typical of tropical climates (Onorato et al. 2011a).

## HOW DID COUGARS USE THE LANDSCAPE COMPARED TO WOLVES?

To gain better insight into how cougars used the landscape relative to wolves, we used DW cougar and wolf locations in a logistic regression, with the same set of resource variables as in our previous analysis. Again, we split analyses into summer and winter seasons.





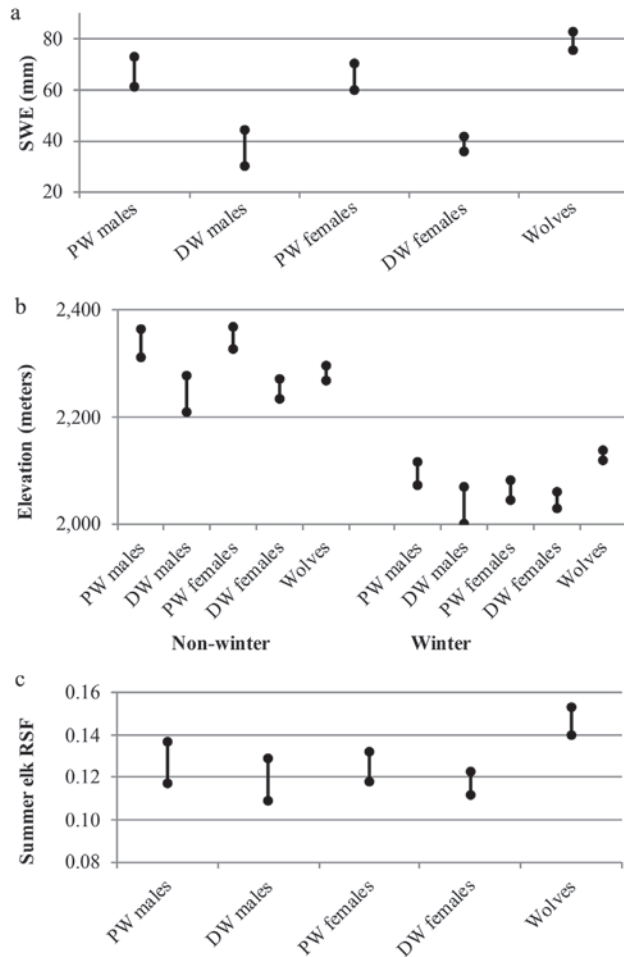
**FIGURE 11.12.** Distribution of the distances of cougars from forested and rough terrain in winter (a) and summer (b) on the Greater Yellowstone Northern Range during wolf presence, 1998–2006. Distributions are number of successful GPS locations obtained during winter day ( $n = 2,017$ ) and night ( $n = 4,680$ ) and during summer day ( $n = 3,982$ ) and night ( $n = 3,732$ ).

The pattern of habitat use by cougars showed clearly that compared to the areas preferred by their dominant competitor, cougars favored rough terrain, were 6–7 times more likely than wolves to be in forested areas, and were 1.5 times more likely to avoid deeper snow (tables 11.7 and 11.8; figs. 11.13, 11.14, 11.15). Cougars traveled and bedded in areas with snow depths averaging 15–25 centimeters and at elevations averaging 2,040 meters—almost 100 m lower than where wolves tended to be, at elevations averaging 2,120 to 2,140 m (fig. 11.13a, 11.13b). Wolves frequented areas with snow depths averaging 33–51 inches. Undoubtedly, less snow makes travel easier for carnivores yet, prior to wolves, cougars did not avoid deep snows to the extent they did during wolf presence, although PW cougars remained close to escape cover (fig. 11.7c). In

fact, PW cougars used areas with snow depths and elevations more similar to areas frequented by wolves, lending further support to the notion that cougar avoidance of wolves was resulting in habitat partitioning by the two carnivores [9].

Bars indicate odds and 95 percent confidence intervals. Variables shown were included in top logistic regression models ( $\Delta AIC \leq 2.0$ ). Variable interpretation is as follows: forest is relative to in versus out of forest, roughness is relative to an increase equal to the maximum used, elk use is relative to an increase equal to the upper 95 percent CI of the mean used, and snow water equivalent is relative to a 2.54 centimeter increase (equaling 13–18 centimeters) in snow depth.

Some cougars in our DW study moved from higher to lower elevations during winter, but as a whole the cougar study population used lower elevations than did wolves (fig. 11.13b). Where cougars and wolves situate in terms of elevation is related to the orientation of open valleys and rough terrain. In south-central Alberta, Alexander and colleagues (2006) also found that cougars showed a trend in distribution from higher elevation and less rugged terrain in December to lower elevation and more rugged terrain in March. Thus cougars and wolves converged spatially over winter, yet cougars remained closer to escape cover as winter progressed, choosing higher slopes with more rugged terrain and rocky outcrops. Wolves showed a more stable affinity for low elevation and less rugged valley bottoms across all winter months. Similarly, in the Madison Valley, Montana, probability of cougar occurrence increased on south aspects and steeper slopes and decreased at lower elevations, while wolf occurrence increased on south aspects, in riparian and grassland habitats, and at lower elevations (Atwood et al. 2009). In the Madison Valley and south-central Alberta studies, valley bottoms were situated at lower elevations compared to surrounding rough terrain. On the Greater Yellowstone Northern Range, the large, open valleys preferred by wolves—the Blacktail Deer Plateau, Buffalo Plateau, Slough Creek Valley, and Lamar Valley—were situated at elevations above 2,100 m on average and 85 to 100 m higher than terrain preferred by cougars during winter. Although we noticed that wolves did not completely avoid the steep, rugged, and forested terrain preferred by cougars, wolves used such terrain infrequently. While distance to escape cover was not included in our top models (forest cover was the more important of those two correlated variables), wolves associated more than cougars



**FIGURE 11.13.** Mean values and 95 percent confidence intervals of snow water equivalent (a), elevation (b), and elk habitat (c) based on a resource selection function (RSF, see appendix E) used by pre-wolf cougars, cougars during wolf restoration, and wolves on the Greater Yellowstone Northern Range, 1987–2005.

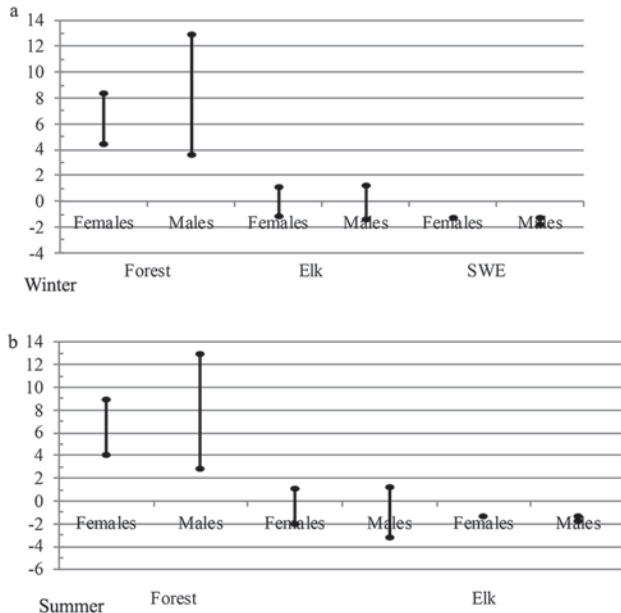
with open grassland and remained farther from forested and rough terrain (fig. 11.15a, 11.15c).

Elk use was included in our top winter models, but the variable was difficult to interpret. At the landscape scale of analysis, the similarity in elk use likely reflected that both carnivores required access to prey while the carnivores overlapped on winter range. During summer, however, cougars were 1.5 to 2 times less likely to use areas of average elk use than were wolves (fig. 11.13c). Cougars also avoided areas and habitats favored by wolves, and this avoidance potentially constrained the cats' access to areas of greater use by elk.

## COUGAR DISTRIBUTION CHANGES BEFORE AND FOLLOWING WOLF RESTORATION

The ability to map animal populations accurately is essential for understanding the spatial dynamics of interactions between resources and species, for understanding key ecosystem processes, and for effective conservation planning (Frair et al. 2007; Holdo and Roach 2012). Our synoptic habitat results allowed for specific quantitative comparisons between the PW and DW study periods as well as enabling us to produce maps of cougar activity within the two time frames. To illustrate the influence of wolf restoration on the distribution of cougars across the Greater Yellowstone Northern Range, we used the synoptic models to generate maps depicting the probability of cougar occurrence before and during wolf restoration. These maps depict the probability of cougar use scaled from no use, or 0, to high probability of use at 1.0, but do not indicate areas of increased or decreased use between the two time frames. To understand better whether cougars used areas more, less, or equally during wolf presence, we subtracted the scaled map of cougar use prior to wolf restoration from the scaled map of cougar use during wolf restoration. We mapped the result of this subtraction for each season, indicating areas of increased cougar use during wolf restoration in warm colors and areas of decreased cougar use in cool colors (fig. 11.16).

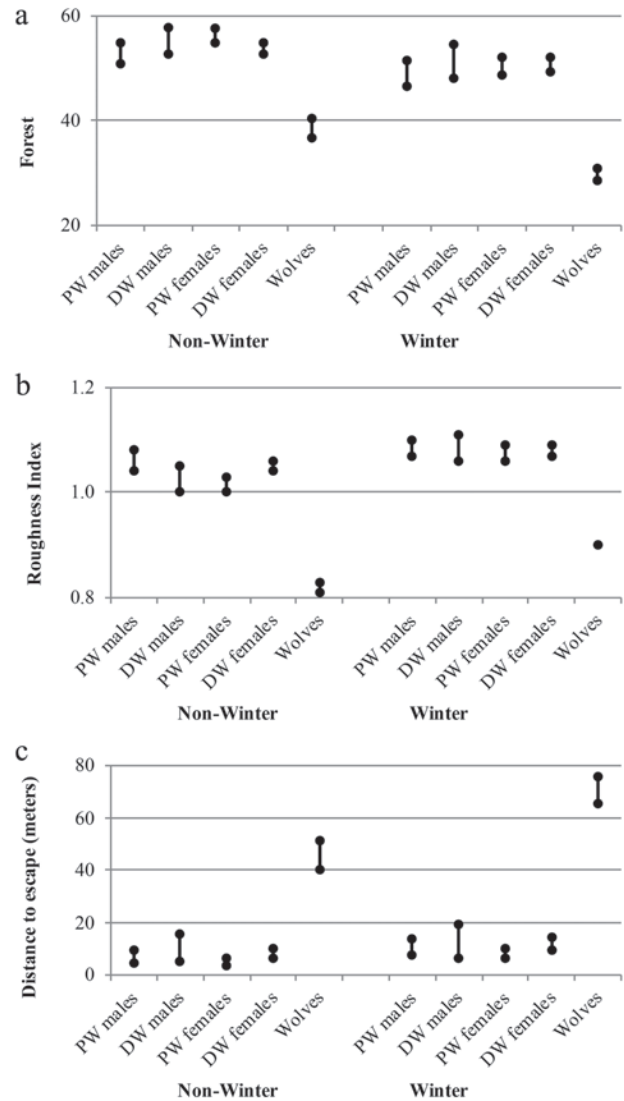
As the cougar population was growing prior to restoration of wolves, we expected cougars first to settle and fill in *optimal habitats* that provided prey and cover (see table 9.1; Murphy 1998). If the population continued to grow or reached carrying capacity in optimal habitats, new cougars immigrating into the area should then be relegated to more *marginal habitat* that provided less than ideal food and cover (Ward 1987; Stamps 2001) at the periphery of the most suitable areas—with a resulting increase in overall spatial extent (see Danchin et al. 2001; Stamps 2001; Breininger and Carter 2003). Instead, as wolves were restored across the Greater Yellowstone Northern Range, cougar preference for habitats that provided security and cover increased, and the overall spatial extent used by adult cougars contracted by 10 percent to 46 percent for females and 43 percent to 65 percent for males in both summer and winter (fig. 11.17). Some areas were hotspots, such as the Black Canyon of the Yellowstone River, which provided optimal habitat for cougars prior to wolves and was used more intensively by cougars after wolf restoration. In winter such areas were



**FIGURE 11.14.** Cougar resource use relative to wolf resource use in winter (a) and summer (b). Values above one indicate greater odds of use, and values below one indicate lower odds of use. For example, cougars were roughly one and a half times less likely to use areas with 13 to 18 centimeters of snow depth compared to areas with no snow (common on south-facing slopes and forested areas at lower elevations along the Black Canyon of the Yellowstone) during winter compared to areas used by wolves.

generally at lower elevations with less snow, mostly along river and creek corridors (fig. 11.16a). This concentration of cougars in preferred habitat resulted in a greater number of cougars using a much smaller portion of the Northern Range, while a decline in use occurred in other portions. Figure 11.16 also reveals portions of the study area with little change in use—mainly in areas little used by cougars in either study phase.

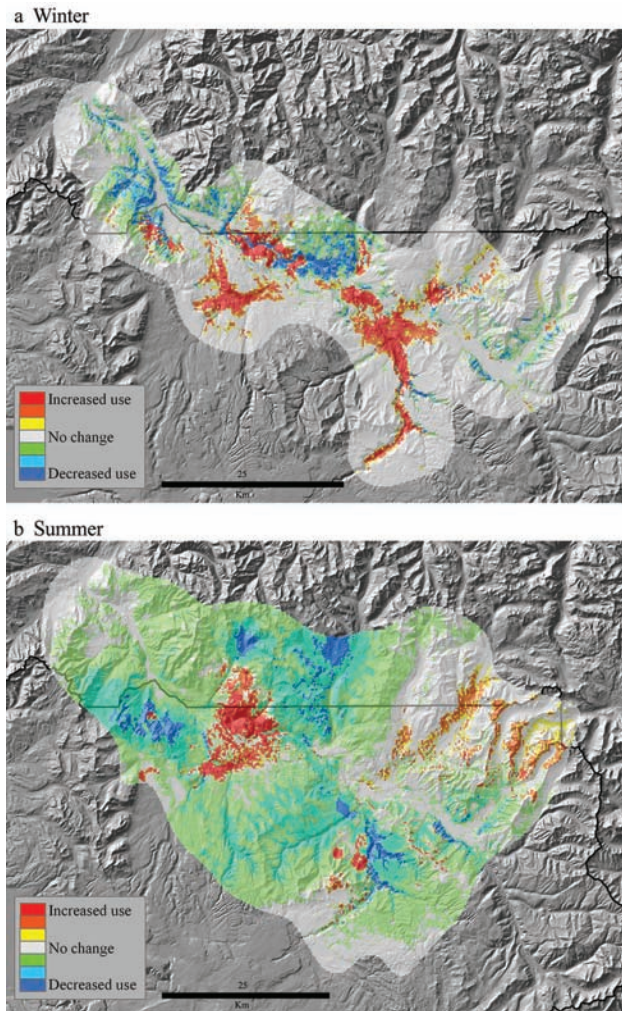
Our findings that cougars primarily used similar habitat during wolf colonization but oriented more toward those types that provided greater security, coupled with a contraction of space use on the Greater Yellowstone Northern Range, was consistent with the hypothesis of a strong effect of exploitative and interference competition with wolves (see hypotheses 3 and 6 in table 9.1). Cougars maintained a similar basal niche by shifting into similar habitat, but the existence of a new competitor precluded use of some areas and caused a retraction in the collective use of the study area.



**FIGURE 11.15.** Mean values and 95 percent confidence intervals of forest (a), topographic roughness (b), and distance to escape (c) used by pre-wolf cougars, cougars during wolf restoration, and wolves on the Greater Yellowstone Northern Range, 1987–2005.

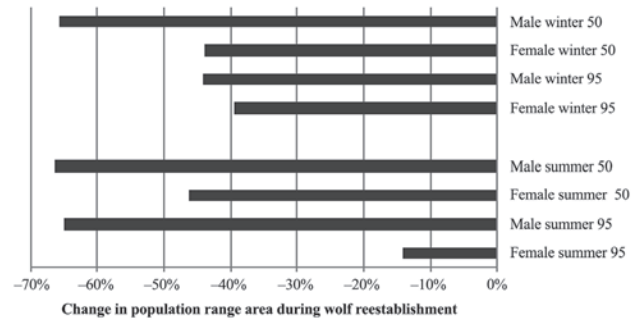
Another explanation for a contraction in range requires examination. The space required for cougars to survive and support offspring might also contract if they have greater access to key prey resources, which would occur if prey abundance increased or if prey also used the landscape differently during wolf restoration (Anderson 1983; Seidensticker et al. 1973; Hemker et al. 1984; Comiskey et al. 2002). Yet elk that occupied the Greater Yellowstone Northern Range and





**FIGURE 11.16.** Change in cougar use of the Greater Yellowstone Northern Range during winter (a) and summer (b) as a result of subtracting cougar spatial use during wolf restoration from cougar spatial use prior to wolf presence, based on probability of use from our synoptic models and set to a 95 percent contour. In winter, cougars concentrated use along the river canyons to a greater degree than prior to wolves. Areas of little change (light gray shading) also represent places cougars rarely used in either study phase.

the Madison River drainage of Yellowstone did not substantially alter their habitat selection and movement patterns after wolf restoration (Mao et al. 2005; Kauffman et al. 2007; White et al. 2009c: 465). During wolf restoration, elk abundance and calf:cow ratios were lower than prior to wolves, and areas used by cougars reflected low elk use. Given these conditions, cougars would benefit from having a home range



**FIGURE 11.17.** Overall percent decline in core area (50%) and total area (95%) used by all adult male and female cougars after wolf restoration. Percent difference was determined by comparing to the area within 50 percent and 95 percent contours used by all adult male and female cougars prior to wolf restoration. We calculated area based on results of the individual synoptic modeling method combined for each sex, season, and phase.

large enough to shift among patches in which they have not hunted recently, home ranges should overlap less, and ranges should be less stable than they were during the PW study when prey numbers were much greater and more predictable. Male home ranges should then also increase as females become more dispersed on the landscape. Contrary to these expected outcomes, female home ranges and core areas remained stable in size, and their home ranges overlapped to a greater degree. Furthermore, adult female cougars did not shift home ranges very much but instead maintained fidelity to home ranges after wolf restoration. Therefore the hypothesis that cougars might require less space to survive and support offspring resulting from greater access to key prey resources had little support in explaining the observed contraction in use of the study area.

## SUMMARY

Our analyses show how space-use dynamics of cougars are related to landscape characteristics and dynamics of snow, elk use, and wolf use. These analyses emphasized the importance of forested and rough terrain for cougars, both within their home range and in situating their home range in the study area before and during wolf restoration. As wolves recolonized the Greater Yellowstone Northern Range, cougars remained in or very near forested and rough terrain with low accumulation of snow, more so than prior to wolf presence. In winter cougars clearly avoided wolves—males more so than females. The onset of summer relaxed the con-



straints from wolves to some degree, although cougars still avoided areas used most heavily by wolves. By remaining in areas that provided greater security, cats traded off opportunities to hunt in prime elk habitat. Female cougars took greater risks and ventured farther from escape cover within their summer home ranges but remained closer to cover when on the periphery of those ranges. Given their need

to hunt more often to support kittens, female cougars were more constrained by high wolf use compared to male cougars. These habitat preferences and the mosaic of habitat on the Greater Yellowstone Northern Range enabled cougars to mitigate competition risk and seek refuge from competitors and no doubt helped cougars survive in a landscape where wolves and bears dominate.

## CHAPTER 12

### Synthesis

#### *Competition Refuges and Managing Risks in a Wolf-Dominated System*

When taken together, our findings from chapters 10 and 11 indicate the effects of wolf restoration on cougar spatial arrangements and habitat selection (summarized in table 17.2, chapter 17). In this chapter we explore how cougars managed competition risk from wolves while maintaining access to prey and mates. We address how landscape heterogeneity might influence habitat partitioning and coexistence of cougars and wolves on the Greater Yellowstone Northern Range. Finally, we discuss potential outcomes for cougars when sharing the landscape with wolves.

#### **MANAGING COMPETITION RISK WHILE OPTIMIZING ACCESS TO FOOD AND MATES**

What is known about the habitat preferences of cougars in the western United States makes it clear that they show affinity for rugged terrain with forested or woody cover and are generally averse to crossing or otherwise using flat, open areas (Logan and Irwin 1985; Koehler and Hornocker 1991; Laing and Lindzey 1991; Williams et al. 1995; Riley and Malecki 2001; Dickson and Beier 2002; Mattson et al. 2007). Although broadly consistent with these findings, our results revealed that when cougars shared the landscape with dominant competitors, remaining in or near escape cover was of paramount importance—particularly in late winter as increasing snow depth and prey movements increased spatial overlap with wolves. Cougars avoided wolves by strengthening their use of forested, rough terrain situated at lower elevations along river corridors, including the Black Canyon of the Yellowstone near Gardiner, Montana, the Grand Canyon of the Yellowstone near Tower Falls, and along the Lamar River adjacent to its confluence with the Yellowstone River. After wolf restoration, cougars showed increased affinity for these habitats at both scales of our analyses and during both seasons.

Cougars also more strongly avoided wolves during winter, probably because wolves more consistently traveled through cougar home ranges while the two carnivores were overlapped on ungulate winter range, resulting in increased risk of encounter. Wolf use values during winter translated to a low of 29 to a high of 89 wolves per 1,000 km<sup>2</sup> (average of 58/1,000 km<sup>2</sup>)—some of the highest winter densities observed compared to other wolf populations (see Fuller et al. 2003: 167, table 6.2). In other studies wolves reached an upper density of 40 to 69 per 1,000 km<sup>2</sup>, with reports of a onetime density as high as 92 wolves per 1,000 km<sup>2</sup> on Isle Royale, Michigan, in 1980 (Pimlott 1970; Peterson and Page 1988; Fuller et al. 2003: 170; Cariappa et al. 2011). In conjunction with the rising wolf density from early restoration through colonization on the Greater Yellowstone Northern Range, we increasingly encountered wolf tracks in the rugged terrain associated with prime cougar habitat. While wolves displaced cougars from kills most commonly in winter, sometimes resulting in cougar death, bears were more frequent visitors to cougar kills during spring and summer. With wolves and bears largely dominating the Northern Range, compared to the PW period, cougars were using the landscape under the competing constraints of managing competition risk and optimizing access to food and mates.

#### **Protection of Young and Access to Mates**

Because female cougars were frequently supporting offspring, they should have oriented toward rough terrain for protection of young and avoided wolves more than did males. As wolves were restored, female cougars did show greater affinity for rough terrain in summer compared to males and compared to PW females, but they did not avoid wolves to the extent we expected.

Female cougar response to summer wolf use and density on the Greater Yellowstone Northern Range may be a reflection of the tradeoff between accessing high-quality hunting habitat, necessary for providing for young, and minimizing their risk of wolf encounters. During summer most females selected for intermediate ranges of wolf use while using lower and higher wolf use areas less (see figs. 11.8c, 11.9b). Subordinate cougars might perceive low and high densities of wolves as poor-quality habitat, with low wolf density corresponding to low quality of resources and high wolf density corresponding to high costs of competition and high mortality risk. Intermediate competitor densities could provide an optimal solution to the tradeoff between poor habitat and competition. The tradeoff between hunting and wolf avoidance apparently necessitated females using areas farther from escape terrain to access prey, supported by the fact that female cougars made kills more frequently outside their core area and farther from escape cover than their PW counterparts. Other studies have demonstrated that competitor density can be used in assessing overall habitat quality in habitat selection and offspring investment decisions, integrating information on resources and competition (Forsman et al. 2002; Forsman et al. 2007). If species use information from competitors, the potential arises for a continuum of possible outcomes from mutualistic to exploitative interactions that may even lead to an “evolutionary arms race” in hiding and acquiring information (Fletcher 2007; Forsman et al. 2007).

During winter and counter to our hypothesis, DW female cougars avoided wolves to a lesser extent than did males. Female cougars did, however, mediate competition risk by remaining in or very near—typically within 30 meters of—escape and hunting cover, which would enhance protection of kittens. Yet there were differences in how females used the periphery compared to the core of their home range. Females ventured farther from escape terrain and moved at a quicker rate when they were within the periphery of their home range. These findings revealed that female cougars apparently required greater access to prey to support offspring, whereas male cougars were more able to avoid wolf use areas.

Female cougars may also benefit by sharing resources with other females within optimal habitat. Maintaining home range sizes similar to those of their PW counterparts yet sharing a greater amount of their home range with other females may be an adaptive advantage in place of grouping

behavior. Sharing with conspecifics prime habitat that provides hunting cover and protection of young from other large carnivores might in fact enhance individual and population fitness. But benefits might only be realized up to the point where resources become limiting, at which point *intraspecific* competition should increase. Females may further maximize their offsprings’ survival, as well as their own fitness, from sharing their area and food with growing offspring for longer periods of time before causing young to disperse. Larger offspring with more experience would enable increased detection of and perhaps defense from competitors, a topic to which we return in later chapters.

Unlike females, male cougars did not exhibit selection for a midrange of wolf use during summer and instead exhibited a monotonic increase with increasing wolf use. We suspect this occurred because home ranges of males were already situated in highly secure areas; they used rough terrain to a greater extent than did females. Further, by using competition refuges and strongly avoiding areas used by wolves during winter, male cougars presumably did not need to use areas closer to escape cover while maintaining access to prey and mates. Males were also more sedentary, typically moving less during the day in winter than females—males averaged 43 meters and females averaged 105 meters per hour. Although they traversed greater distances than females at night, males still selected rough terrain more than did females. Because males do not support offspring, they did not have to hunt as frequently, thereby exposing themselves to lower risk of wolf encounters than females.

Growing evidence from various systems indicates that male cougars use more rugged terrain than do female cougars (Arundel et al. 2007; Webb et al. 2011). On the Greater Yellowstone Northern Range, the affinity of males for rough terrain—particularly during winter, when greater overlap between genders and peak breeding in February through April occurred—suggested to us that males sought out more secure cover when territorial defense needs and potential encounters with other males should be greatest. While together, cougar pairs frequently vocalize and are likely distracted during courtship and breeding; thus staying in complex terrain may aid in minimizing their detection by competitors. Post-wolf restoration, we encountered a male and female during breeding on at least five separate occasions. In all these encounters the pair was in a topographically complex and rocky area and, excluding one encounter, we did not

hear the cats vocalizing until we had approached within 100 meters or less of their location. From the security of cover, we listened to repeated yowling, or “caterwauling,” from the pair and observed as females rolled in front of males.

But why should PW males select for rough terrain (six times more likely in winter and twelve times in summer) more than male cougars during wolf restoration? Two explanations seem possible: (1) that PW males selected rough terrain as security from other males and (2) that DW males required access to less available prey within their home ranges, so they had to venture farther from rugged terrain. The younger age structure and greater social instability in the PW study phase perhaps meant that less experienced males sought out protection from other male cougars in rougher terrain to a greater degree than the older, more experienced males in our DW study needed to do. Males during wolf restoration ventured farther from escape terrain but used less edge landscape in their winter core area than did PW males within their core area, providing conflicting information about access to prey. Dominant resident males may seek opportunities to exclude new, subdominant males. Such behavior would lend support to our premise that new, immigrant males were avoiding conspecific competitors during social instability in the PW study phase compared to DW presence.

### **Acquiring Prey While Avoiding Interspecific Competitors**

Habitats that facilitate hiding or escape provide refuge from competitors, but they may not necessarily provide the best foraging opportunities for cougars (Durant 1998; Creel and Creel 2002). This was the case for wild dogs in the Selous Game Reserve in Tanzania, where researchers discovered that wild dogs preferred deciduous woodland, which was little used by dominant lions but also held low density of prey (Creel and Creel 2002: 251). Similarly, Serengeti cheetahs avoided their competitors and utilized areas with low-density prey (Durant 1998).

The accumulated information on cougar, wolf, and elk habitat selection during wolf restoration indicated that accessing patches that facilitated foraging opportunities was accompanied by increased levels of risk for cougars. Seeking refuge from competition was apparently greatest when cougars were overlapped with wolves during winter. In concert, elk grouping behavior and increased use of open areas devoid

of snow—coupled with lower numbers of adult and calf elk available during wolf restoration than prior to wolves—might have translated to greater difficulties for foraging cougars. During wolf cougars situated their home ranges in areas of lower elk use than did PW cats in winter. But within their home ranges they used elk habitat similarly—perhaps because elk were concentrated at low elevations on winter range. Although cougars remained relatively close to habitats that provided increased security, they secured prey farther from forested, rough terrain, as evidenced by where they made kills in the DW compared to the PW study (see fig. 5.13). Some differences in where cougars killed prey were a result of cougars having less access to elk calves, as the calf to cow ratio declined during the study. Adult elk were killed on gentler slopes at lower elevations and farther from escape cover than were smaller ungulate prey, and such areas had greater use by wolves. Both the longer time cougars spent at large kills and the greater visibility of these kills translated to greater risks for cougars of displacement by wolves and bears. Also potentially increasing wolf encounters of cougar kills was the fact that multiple wolf pack territories overlapped winter hunting grounds on the Northern Range—a situation that did not conform to the widely held conceptual model of distinct territorial boundaries with interstitial prey refuges (Kauffman et al. 2007).

In contrast to winter, during early spring and summer wolves were busy with denning and rearing pups. Their activity was centered around dens and rendezvous sites on lower slopes (Mao et al. 2005). Northern Yellowstone elk migrated away from these areas of concentrated wolf activity and selected habitats at higher elevations that allowed them to obtain abundant nutritious forage (Mao et al. 2005). While some cats followed migrating elk, overall they avoided areas frequented by elk and typically remained at lower elevations within their home ranges than their PW counterparts. Cougars selected areas that provided increased security, but such areas also had low use by elk relative to the areas favored by wolves (fig. 11.12). Despite our findings that female and male cougars did not avoid wolves to the same degree in summer as during winter, they still preferred areas that were typically less used by wolves, and both genders ventured farther from escape cover than their PW counterparts.

Counter to the idea that wolves always out-compete cougars by limiting cougars' access to certain habitats and prey, might wolf predation also have facilitated cougar predation



on elk (Bowyer et al. 1999; Kunkel et al. 1999; Atwood et al. 2007; Gower et al. 2009a; Murphy and Ruth 2010)? Studies conducted so far on the Northern Range have not yielded empirical support for profound elk habitat shifts relative to wolf presence (see Mao et al. 2005; Kauffman et al. 2007). On the Greater Yellowstone Northern Range, elk often cannot separate themselves from wolves during winter but rely on other behaviors to reduce predation risk (Mao et al. 2005). In fact, locations of wolf territories were a positive predictor of elk habitat use. Wolf and elk distributions closely overlapped, and elk did not avoid core areas of wolf territories (Fortin et al. 2005; Mao et al. 2005). Preference by elk for areas also selected by wolves likely reflected elk's continued need to access high-quality forage, especially during critical winter months when elk and other ungulates experienced diminishing fat reserves (Cook et al. 2001; Creel et al. 2005; Mao et al. 2005; Kauffman et al. 2007; White et al. 2009a, 2009b). In addition, there was little support for changes in the types of habitats where wolves killed elk over ten years after restoration, an expected response if elk altered their habitat selection and movement patterns to avoid encountering and being killed by wolves (Kauffman et al. 2007).

The ability of elk to mediate predation risk in dynamic ways may also explain why they do not avoid the riskiest habitat patches (Creel et al. 2005; Fortin et al. 2005; Mao et al. 2005; Kauffman et al. 2007). Elk mediated risk of predation from wolves through small-scale movements, increased grouping behavior and activity patterns, or the use of landscape features—open, windblown patches devoid of snow—that provided effective escape from predators (Mao et al. 2005; Bergman et al. 2006; Kauffman et al. 2007; White et al. 2009c). Elk behavior in response to wolves also depended on the level of wolf use they experienced (Fortin et al. 2005). At low and medium wolf densities, elk preferred open areas and aspen stands over coniferous forests. Greater habitat shifting by elk occurred in areas with higher wolf use. Although elk did not avoid traveling in high wolf use areas, they preferred conifer forests when traveling through these areas (Fortin et al. 2005). Traveling through timber may have facilitated predation by cougars at certain times, but steep slopes preferred by cougars impeded elk movement and may have reduced the possible effect of facilitating cougar predation on elk. Although elk responded to the risk of wolf predation with increased vigilance or shifting habitat use temporally, such anti-predator behaviors have not brought about landscape-

level changes in the distribution or behavior of elk during winter (Laundré et al. 2001; Fortin et al. 2005; Gude et al. 2006; Kauffman et al. 2007).

Yellowstone cougars certainly remained effective at killing elk in areas associated with low elk use, but overall we found little evidence that wolves facilitated cougar access to prey during winter. During wolf presence, cougars made kills farther from forested and complex terrain than did PW cougars, exposing them to greater risk of displacement, which contrasts with predictions if wolves facilitated cougar predation. Perhaps cougars can find sufficient food in areas used less by prey overall, so there is no need for them to favor high prey use areas. In other words, low prey abundance does not necessarily equate to poor hunting. If at low densities or in more forested terrain elk form smaller groups, then those groups are less likely to become alerted to a cougar's slow stalk and short-distance ambush. Thus cougars may benefit by exploiting lower densities of prey, as it allows them also to avoid the high densities preferred by their competitors (see Durant 1998).

### Information Cues and Adaptive Behaviors

Evolving over a long history with large competitors, cougars maintained selection for behaviors that placed them in and near habitats that provided escape, but individuals may also quickly develop knowledge about wolf presence from various information cues. The shift in distribution of cougars, their avoidance of high wolf use areas, and their relatively stable home ranges within secure habitats all suggest that cougars quickly adapted to wolf presence and responded to reduce interactions with wolves, perhaps shortly after wolf restoration in 1995 and 1996.

To gain information about the spatial distribution of their competitors, subordinate cougars likely used visual, auditory, and olfactory cues to identify and avoid areas of high wolf use (Sih 1992). Such information gathering is often proportional to activity. More active animals, such as wolves, are more conspicuous in terms of visual, sound, and chemical cues (Barbosa and Castellanos 2005). A wolf's howl can carry over great distances (Harrington and Mech 1979; Harrington and Asa 2003; Mech and Boitani 2003a). Like bobcats, which immediately ran for the nearest dense vegetative cover after hearing a playback of coyote calls (Wilson et al. 2010), cougars, too, may steal away into or remain near forested, rugged habitat.

During both day and night, cougars made adjustments to wolf presence by exploiting the safest habitats. Wolves foraged more cohesively during winter but also generally had a more aggregated distribution than in summer. Consequently, a cougar that moved away from wolves once they were seen or heard had a better chance than average of moving into an area with lower competitor densities (Colegrave 1997; Durant 2000). Using complex habitat might also hinder wolves by impeding their ability to maneuver through terrain features that cougars readily and rapidly traverse (Frampton et al. 1995; Clark and Messina 1998; Denno et al. 2005). Because there is no benefit to staying in dangerous areas when resting, cougars should rest in the safest habitats, especially during seasons when competitors are most common. Remaining inconspicuous while resting in day beds or hiding in refuges should also translate to reduced encounters with competitors.

By adopting behaviors to avoid wolves, cougars could help ensure that mortality from direct interactions with wolves occurred infrequently, yet cougars were not always successful at avoiding wolves. Interactions with wolves, including displacements from kills and the deaths of three cougar adults and five kittens, occurred primarily in winter. Adult cougars' familiarity with habitat in their home ranges should have provided a relatively high probability of escape when chased by wolves, as cougars typically remained close to escape cover. For at least two cougars, F106 and M127, this was not the case, as both were killed by wolves in or very near forested, rugged terrain. Their stories reveal that subtle cues associated with an individual's health or other unknown factors could affect outcomes of interactions, just as they do between predators and prey. Female 106 (see fig. 15.11) was a healthy, well-established resident with two six-month-old kittens, yet for some reason she failed to detect the presence of and escape pursuit by wolves. Because her kittens were stashed well away from where the interaction occurred, it did not appear that F106 was killed while defending them. She may simply have been caught by surprise. Male M127 was chased downslope and mauled over at least 60 m of forested terrain. Although he attempted to tree on several occasions, he had difficulty doing so because of an injured leg that was still mending. We knew this from having captured him almost nine months earlier and having observed his difficulty at remaining in the tree from which he leaped to seek refuge within a complex of boulders. As we assessed his



**FIGURE 12.1.** Adult male cougar M127 was mending from broken tarsals and metatarsals in his left leg when captured on March 1, 2004. The injury hampered his ability to climb and likely played a role when he was chased through an area with trees, captured, killed, and consumed by the Geode pack on November 21, 2004. Photo by Toni Ruth, Wildlife Conservation Society.

condition while replacing his collar, we discovered mending broken tarsals and metatarsals in his left leg (fig. 12.1).

## COMPETITION REFUGES AND COEXISTENCE

The outcome of competition for prey and space should depend on the relative abilities of carnivores and prey to respond to each other spatially as well as the relative costs and benefits of responding (Barbosa and Castellanos 2005). Not only is the use of different habitats the most common form of resource partitioning between similar species, but research in various systems suggests that habitat complexity and behavior combine to structure ecological communities by reducing interference interactions (MacArthur and Wilson 1967; Schoener 1974; Denno et al. 2005; Hughes and Grabowski 2006). In particular, heterogeneous landscapes provide opportunities for competitively inferior species to escape competition by using a different type of habitat patch





**FIGURE 12.2.** *Interspersed with the large open valleys and plateaus on the Greater Yellowstone Northern Range, topographically complex areas and tree cover enabled cougars to move along or near edges adjacent to areas of greatest wolf activity. Such areas served as refuge from competition, where wolves had greater difficulty pursuing cougars and cougars had greater potential to seek refuge in trees or rock outcrops. Photo by Jason Husseman, Idaho Department of Fish and Game.*

or by finding empty patches that result from clumped distributions of competitors (Janssen et al. 2007; Schröder et al. 2009; Foster et al. 2010). Subordinate species can persist by seeking out and using *competition refuges*, and the invasion success of dominant competitors is reduced (Durant 1998; Denno et al. 2005).

The heterogeneous landscape present on the Greater Yellowstone Northern Range provided opportunities for cougars to seek refuge away from wolves and enabled interspecific habitat partitioning. Attributes of the Lamar Valley and the Blacktail Deer Plateau—large, open grasslands and windblown snow deposition—were preferred by wolves

and apparently represented particularly high competition risk (wolf density there averaged 70 to 80/1,000 km<sup>2</sup>; White et al. 2010), while other zones, such as the Black Canyon and Mount Everts, more likely represented lower risk for cougars (wolf density averaged 30/1,000 km<sup>2</sup>).

Consistent with our predictions, cougars overall were better exploiters of steep, rocky terrain and forested habitats than were wolves. Adjacent to and interspersed with the large open valleys and plateaus, topographically complex areas and tree cover—including such habitats along river corridors—enabled cougars to move along or near edges adjacent to areas of greatest wolf activity (fig. 12.2).

Such areas served as refuge from wolves, as the canids had greater difficulty pursuing cougars while cougars had greater potential to seek escape in trees or rock outcrops. As a consequence, mortality caused by wolves may be low at any given time because avoidance was effective, a finding similar to that noted for bobcats and African cheetahs that used refuges to avoid their dominant competitors (Durant 2000; Wilson et al. 2010).

The distribution of limiting resources can also define where animals locate spatially in an ecosystem (Ford 1983; Mitchell and Powell 2004; Gower et al. 2009b). In systems where wolves are becoming reestablished or have been restored, refuges from competition may serve as the limiting resource for subordinate cougars. As a result, cougars might compete to occupy those portions of the landscape where there is significantly reduced risk of encountering wolves or where enough rugged and forested habitat exists to enable escape when an encounter does occur, resulting in greater “packing” of cougars into optimal habitat. Once too many individual carnivores are crowded into an area, the carrying capacity of a given habitat can be exceeded, and competition for and overuse of resources can then transform an optimal habitat into one of lower quality (Gibson 1994). Such increased competition for a limited set of resources may then affect the entire population, with competition among conspecifics becoming more intense and costlier than competition with other species.

With a greater number of cougars crowded into a given area of habitat that provides fewer elk on the Greater Yellowstone Northern Range, we might expect increased probability of encounters with conspecifics, including adults killing younger individuals, hastened dispersal of offspring out of their natal area, and decreased security for maternal females and kittens from adult male cougars, since encounter rates with males might increase (Lima and Dill 1990; Losey and Denno 1998; Creel et al. 2001). We did not observe these outcomes during our study. Infanticide was extremely rare, and mortality of adult females from aggressive encounters with males did not occur in our DW study. We documented only one older adult male killed as a result of fighting; thus direct aggressive contact between adult males appeared to occur rarely. The lack of intraspecific strife we documented further suggests that male cougars found a way to exploit exclusive home ranges without spending substantial energy in their defense.

Such tolerance among conspecifics could change if within limited refuges from competition, access to prey also becomes limited. Even in the event that prey become limiting and competition with wolves and bears for live and dead prey increases, the costs of intraspecific competition may not outweigh the benefits of sharing resources with familiar conspecifics. That is, cougars may continue to invest more in avoiding the dominant competitors and be less concerned with avoiding one another. Ruth (2004a) suggested that this was the case in the North Fork of the Flathead River, where cougars competed with wolves and bears during both summer and winter, and starvation was a considerable cause of mortality. Kortello and colleagues (2007) also noted cougars in poor condition during their study but did not report on aggressive interactions between conspecifics.

## COMPARISON TO OTHER SYSTEMS

Where cougars and wolves have shared the landscape for long periods—at least ten years—some studies report that these two carnivores are able to coexist because of resource partitioning that enhances niche separation. In other studies, researchers have reported little separation in habitat and prey use and thus a lack of resource partitioning, suggesting that cougars and wolves share the landscape with little competition (Kunkel et al. 1999; Ruth 2004a; Webb et al. 2011). Strong spatial-habitat partitioning reported in some studies and a lack of spatial-habitat partitioning in others might be explained by considering landscape heterogeneity or homogeneity, including prey diversity, in various systems.

There are several systems in which habitat complexity promoted coexistence of predator and prey (Turchin and Kareiva 1989) and of dominant and subordinate competitors (Durant 1998; Scognamillo et al. 2003; Finke and Denno 2006; Foster et al. 2010; Wilson et al. 2010). For instance, where pumas and jaguars were sympatric in mosaic landscapes, pumas reportedly used more open habitats, while jaguars preferred forested cover over exposed areas (Scognamillo et al. 2003). Temporal heterogeneity, whereby species aggregate, move, and aggregate again in different localities, sometimes acted in concert with spatial heterogeneity. Cougars in Banff National Park, Alberta, Canada, showed temporal avoidance of areas recently occupied by wolves (Kortello et al. 2007). Another example comes from the Serengeti where, during the dry season, hyena densities were relatively low and cheetahs did not need to avoid hyenas actively (see



Durant 1998). However, when the plains were occupied by large numbers of hyenas during the wet season, cheetahs adjusted their activity patterns to avoid both hyenas and lions. In addition, Serengeti cheetahs were more likely to be found close to other cheetahs than to hyenas or lions in both the dry and wet seasons, which suggested that competition with other species was more intense than competition with conspecifics (Durant 1998). Heterogeneous landscapes that enable partitioning of habitat and terrain features may also reduce the need for competitors to partition other resources, such as food, as long as prey does not become limiting. Cougars and wolves on the Greater Yellowstone Northern Range may have exploited similar prey with little dietary differentiation because the intermix of rugged terrain and open grasslands provided ample opportunity for habitat partitioning between cougars and wolves.

In contrast, homogeneous landscapes appear to limit opportunities for interspecific habitat partitioning, and competitors might use space and habitat more similarly, with their coexistence depending more on dietary segregation (Foster et al. 2010). Harmsen (2006) analyzed seven published studies of sympatric jaguars and pumas and reported that their diets overlapped by ~80 percent in heterogeneous habitats but were dissimilar (~20 percent overlap) in more homogeneous, closed rainforest environments. Yet such a dichotomy does not hold up well when examining data from the North Fork of the Flathead River, Montana, where homogeneous habitat structure and little apparent partitioning of habitat would suggest that cougars and wolves should select different types and sizes of prey. Instead, wolves and cougars selected for prey of similar species, age, sex, and condition (Kunkel et al. 1999). Similarities in diet potentially arose from wolves adapting their hunting behavior to conditions imposed by the landscape. In the dense vegetation and homogeneous structure of the North Fork, wolves adopted a hunting style more similar to that of cougars and stalked prey to closer distances than is common in mosaic habitats, which enable wolves to pursue prey over longer distances (Kunkel et al. 1999).

Homogeneous habitat that provides more continuous canopy cover and dense vegetation is further hypothesized to reduce the frequency at which avian scavengers locate prey carcasses, thus reducing direct encounters and perhaps relaxing the need for cougars to partition habitat with wolves, as was observed in Glacier National Park (Creel 2001; Ruth 2004a). Yet there, not unlike our findings for the heteroge-

neous landscape of the Greater Yellowstone Northern Range, wolves visited and scavenged from 26 percent of documented kills and displaced cougars from another 10 percent of documented kills during winter (Ruth 2004a). Smaller winter range, which increases the overlap of cougars and wolves, may be one explanation for wolves encountering kills in the Glacier study. However, ravens and other scavengers may also have adopted behaviors that enhanced their search efficiency for carrion in contiguously forested landscapes.

Diversity and abundance of prey also play a role in the ability of carnivores to partition prey and perhaps habitat. For instance, deer were the most abundant prey in the study on the North Fork of the Flathead River, so prey size likely drove the lack of dietary differentiation between cougars and wolves that would have been expected if elk were the primary prey. Further, northern temperate systems are associated with relatively low prey diversity when compared to the closed forests of the Neotropics, which have a greater diversity of prey, enabling greater dietary differentiation between predators in the more homogeneous habitats of southern latitudes (Núñez et al. 2000; Maxit 2001; Polis et al. 2003; Scognamillo et al. 2003). In milder climates smaller prey are not only more abundant but available year-round. Northern latitudes like the Northern Range hold a significant amount of prey biomass, but cougars and wolves were more limited in their choice of prey.

Assessing resource use where species co-occur advances our knowledge of complex interactions, but experimentally adding or removing one of the competitors, as in our study, sheds light on the way the subordinate competitor may initially respond and make adjustments to avoid the dominant competitor. What our study has revealed—and others support this—is that where habitats allow and prey are not limiting, cougars are able to reduce competition with wolves in various ways. Differences in landscape structure should influence behavioral responses as animals adapt to local conditions, which might then alter the effects of carnivores on one another and on their prey as well as overall stability in predator-prey-competitor dynamics (Foster and Endler 1999; Fryxell et al. 2007; Gower et al. 2009a, 2009b).

## SUMMARY

As wolves became restored on the Greater Yellowstone Northern Range, the distribution of cougars condensed, resulting from their more intensive use and sharing of the

most secure habitats. Habitats that provided greater security for cougars were little used by wolves, which preferred more open terrain. A matrix of habitat types—habitat heterogeneity—on the Northern Range enabled cougars to mitigate competition risk by using competition refuges. This avoidance was strongest in winter, when wolves were more likely to roam in large, cohesive packs and the risk of an encounter was greater compared to encountering less cohesive packs or individuals during summer. However, avoidance came

at a cost, as areas of low wolf use were also areas of low elk use. Females with kittens exposed themselves to greater risk to acquire adequate prey than did adult males or solitary females. After wolf establishment, abundance of prey was not yet limiting, as there was no indication of increased aggression between cougars or of starvation, yet areas that provided refuge from competitors may have been limiting as cougars overlapped highly in habitat that offered them advantages over wolves.

## **PART 4**

### Before and after Wolf Restoration

#### *Cougar Population Characteristics*

The better competitor may exclude the other species even though in a habitat where both normally co-exist an observer might only witness severe competition 1 year in 20.

R. H. MACARTHUR (1972)







## CHAPTER 13

### How Might Wolf Restoration Affect the Cougar Population?

In some areas the boundaries that help define a wildlife population are easily demarcated by landscape features—such as for a group of cougars living in a mountain range separated by miles of open habitat in a mountain desert and basin area (Williams et al. 2002; Mills 2007). However, the long distances cougars and wolves can travel between areas typically blur these lines. The habitat in our study area was contiguous with forested mountains outside the boundaries we set, so when we discuss population dynamics, we are necessarily referring to what was happening over the extent of area we were able to sample. Our interest then focused on the component parts that influenced cougar population performance within our study area and under varying conditions as the ultimate measure of whether competition affected subordinate cougars or both cougars and dominant species in a negative manner (Keddy 2001).

In part 4 we tackle questions of whether wolf restoration impacted cougar reproduction, survival, rates of dispersal and replacement, and, ultimately, population growth. Our working hypothesis was that cougar abundance, survival, and natality would be negatively different from analogous estimates made prior to wolf restoration. Further, differences in numbers and vital rates should be causally related to the presence of wolves. We lay out our main predictions in this chapter and address them in the chapters in part 4 by examining data relative to population parameters for pre-wolf cougars and cougars during wolf restoration, and we make comparisons to the population growth of wolves.

#### REPRODUCTION AND SURVIVAL

Interspecific competition with wolves might affect the fitness of cougars through reduced reproduction and survival via two mechanisms—competition for live and dead prey

and direct mortality during interactions. At the initiation of our DW study, we expected that wolves would locate and displace cougars from their kills and that the rate of displacement would increase with increasing numbers of wolves using the Greater Yellowstone Northern Range. Although generally there is good reason for two species that are roughly the same size to avoid fighting, the risk of lethal injury in confrontations is a reality (see Donadio and Buskirk 2006). Cougars have been killed during these direct encounters at kill sites, as documented in Glacier National Park (Boyd and Neale 1992; Ruth 2004a), but maternal females, their kittens, and independent juveniles are expected to be most vulnerable to direct mortality.

Because maternal female cougars killed more frequently than other social classes (and thus have an increased number of kills on the landscape over time), the chances of encounter with competitors and subsequent costs of displacement or risk of death for the mother and her offspring should be greater than for solitary adult males and females. Direct mortality of vulnerable kittens might result in lower reproductive output and lower population growth of cougars residing in wolf-dominated systems. For instance, 73 percent of mortality of cheetah cubs between birth and independence was a result of predation from African lions, and such reproductive failure from competition contributes to the low density of cheetahs in areas dominated by hyenas and lions (Caro 1994; Laurenson 1994). Hence direct mortality affects both survival and reproductive output, particularly when young or their mothers are killed.

Sometimes subordinate species are displaced into habitats where their rates of encounter with prey are low (Durant 1998; Creel et al. 2001). If elk become more difficult to locate or if fewer calves and fawns are available, a mother may

spend longer amounts of time searching patches of forest as well as traveling to the next one to search. Hunting is already energetically costly and otherwise risky, and a reduction in encounter rates with prey is predicted to carry costs for reproduction and survival. Whether a result of frequent displacement from kills by dominant competitors or increased hunting effort to locate prey, a mother's reduced ability to kill frequently enough to feed her growing offspring could result in smaller litter sizes and lower maternity rates if females are unable to support large litters or produce litters as frequently. Dependent young, including kittens of the year less than twelve months old as well as those between twelve and eighteen months of age, are with their mother at least some of the time and are likely obtaining part, if not all, of their sustenance either through milk or from kills made by the mother (Logan and Sweaner 2001; Murphy and Ruth 2010; Quigley and Hornocker 2010). This translates to high energetic demands placed on the mother (Laundré 2005). In these cases—limited access to prey and displacement from kills—competition for food rather than direct killing can also result in lower reproductive output, as food intake has been linked to the probability of conception in some species (e.g., spotted hyenas; Holekamp et al. 1999). For example, in Masai Mara National Reserve in Kenya, Watts and Holekamp (2008) found that loss of food to African lions rather than direct killing of offspring resulted in lower reproduction of spotted hyenas compared to hyenas living in Amboseli National Park with low density of lions. In other areas a combination of direct mortality and competition for food has been shown to reduce survival, reproduction, and density of subordinate competitors (Caro 1994; Laurenson 1994, 1995; Durant 2000; Creel and Creel 2002).

Juveniles are reportedly more frequently the victims of interspecific aggression than are adults, presumably because they have not yet attained skills and knowledge that reduce risk or help them successfully evade injury during direct encounters (Creel et al. 2001). Following individuals with telemetry, as in our study, is most successful with resident adults, and the fate of dispersing subadults is difficult to monitor; thus mortality of this age group is probably biased low. Because subadults often have low survival rates, even if young cougars are frequently killed by wolves, the mortality may compensate for or replace these other sources of mortality. In addition, like ungulates, juvenile carnivores generally have lower reproductive value than adults—consequently,

births and immigration may absorb some of the mortality with no change in population dynamics. In contrast, if prime-age female cougars are commonly killed, a stronger effect on population dynamics is expected (Creel et al. 2001).

Following from these potential influences of wolf restoration on cougar reproduction and survival, we made the following predictions:

1. We considered that if wolf restoration—a significant change on the Greater Yellowstone Northern Range—altered spatial use by cougars or increased their mortality, thus changing social structure and stability of cougar relationships, then age structure, breeding, and birth patterns might also be altered. Specifically, we expected a similar or younger age structure and less pronounced breeding and birth peaks compared to the pre-wolf period.
2. We expected that frequent loss of food and direct killing of offspring should result in lower reproductive output of cougars compared to cougars living during relatively low densities of competitors prior to wolf restoration. Specifically, we predicted that competition would lead to adult females having smaller litter sizes and lower maternity rates, as females might not be able to support large litters or produce litters as frequently.
3. We predicted that most direct encounters between cougars and wolves would occur at kill sites and that wolves killing cougars and appropriating their food resources would lead to lower survival rates of cougars during than prior to wolf presence. Specifically, we expected that maternal females, their dependent kittens, and subadult cougars might have lower survival rates after wolf restoration than did their pre-wolf counterparts.
4. We expected that interspecific killing would more frequently occur during winter months, a time when cougars and wolves were spatially overlapped on winter ranges of ungulate prey (Ruth 2004a). In particular, dependent kittens should have lower survival in winter than summer as a result of direct encounters with wolves and a potentially undernourished mother being unable to provide sufficient food for offspring.
5. If wolves kill cougars of all ages, then the intensity of wolf use in Yellowstone along with hunter harvest of cougars overlapping the northern park boundary should be main factors explaining variation in survival of adults, independent subadult cougars, and dependent kittens.

## COUGAR POPULATION DENSITY AND GROWTH

There are numerous examples of one or multiple carnivores limiting the abundance of a subordinate carnivore. Wolves limit the abundance of coyotes through direct mortality, particularly directly killing juvenile transients (Fuller and Keith 1981; Carbyn 1982; Dekker 1989; Berger and Gese 2007). Coyote populations flourished across North America following the extermination of wolves, in part because of their adaptability in human-dominated landscapes (Peterson 1995). During the three years after the arrival of wolves in Yellowstone, 25 percent to 33 percent of annual coyote mortality was attributed to wolves. Predation by wolves appeared largely additive to other sources of death, as the coyote population declined by 55 percent and the mean size of coyote packs on the Northern Range dropped by between 40 percent and 45 percent (Crabtree and Sheldon 1999; Berger and Gese 2007). Following wolf colonization on Isle Royale, coyotes disappeared from the island (Peterson 1995). In other systems coyotes are a dominant competitor, and their predation on San Joaquin kit foxes was largely additive to other sources of mortality and thus a strong limiting factor for the endangered subspecies (White and Garrott 1997). African wild dogs and cheetahs are also strongly limited by competition from larger carnivores—hyenas and African lions (Caro 1994; Creel and Creel 2002). In Serengeti, where wild dogs and hyenas have very similar diets, numbers of both hyenas and lions increased with an increasing wildebeest population, while wild dog numbers did not (Creel and Creel 2002).

If wolves negatively affect cougar reproduction and survival as predicted, then—similar to these other examples—the abundance and growth rates of cougars may be limited by their dominant competitors. Because some once suitable habitats are no longer used by cougars, their densities may also be lower when sympatric with wolves. Clearly, it is important to assess densities relative to reproduction and survival to tease out whether wolves affect cougars by limiting their distribution, their growth through reproduction and survival, or both.

Long-range dispersal movements of cougars are essential for population expansion and restoration in former habitats (Thompson and Jenks 2005; Stoner et al. 2007). As a result of increased competition for resources following the arrival of wolves, the contribution of emigrants dispersing from the Greater Yellowstone Northern Range to surrounding areas

might also change. Deaths of vulnerable kittens and juveniles would mean fewer young are available to emigrate from the system. Consequently, competition could limit the degree to which protected areas such as Yellowstone function as net sources for maintaining cougar numbers and genetic diversity across much larger areas.

In mammals, decisions on whether to stay at home or leave are hypothesized to be driven by three main factors: inbreeding avoidance, competition for mates, and competition for environmental resources (Greenwood 1980; Dobson 1982), and more than one factor may motivate dispersal in a given individual (Dobson and Jones 1985). We discuss these forces in detail in chapter 16. In addition, much of the available information suggests that density-dependent dispersal in mammals is fairly common, with most studies reporting a positive effect of population density on dispersal—although dispersal in some species shows a negative or no effect of population density (Matthysen 2005; Armitage et al. 2011).

Subadult male cougars disperse regardless of density, and their dispersal has been suggested to be obligatory, primarily to reduce competition with dominant males as well as for inbreeding avoidance (Logan and Sweanor 2001). Dispersal of female cougars is hypothesized to be moderately density-dependent, as related primarily to competition for resources (Logan and Sweanor 2001, 2010). We expected that if adults do well at avoiding wolves, offspring survive, and there is little room for young cougars to stay in the carnivore-rich environment, then intraspecific competition for mates and intra- and interspecific competition for resources may affect emigration positively. That is, the dispersal of young—particularly subadult females—should increase compared to the pre-wolf period. Yet outcomes may be different, as both high-quality habitat and risk of predation have been found to increase dispersal in some species and, alternatively, to increase philopatry in others (Koenig et al. 1992; Lin and Batzli 2001; Heg et al. 2004; Lin et al. 2006).

Finally, the timing of independence of young is hypothesized to reduce competition for the mother's time and energy required for mating, pregnancy, and rearing more progeny (Logan and Sweanor 2001: 62). Thus kittens should become independent when they are physically able to survive on their own and about the time their mother is ready to breed again. We would expect that a mother living in a highly competitive environment should then force her kittens to leave at the earliest age they are physically able to survive on

their own. Considering these potential outcomes, we made the following predictions regarding cougar dispersal, growth rates, and density, which we address in chapter 16.

1. If food and space are limited by competition with wolves and bears, subadult cougars should disperse at earlier ages than did juveniles prior to establishment of wolves.
2. Increased mortality rates of kittens and subadults—as a result of deaths from wolves adding to other causes of mortality—should reduce the probability of subadults emigrating from the study area. Alternatively, if survival of kittens and subadults remains similar to that of the pre-wolf period, we would expect that subadults should disperse at

similar or higher rates as a result of intra- and interspecific competition for food and space.

3. Lower reproductive rates and survival during wolf restoration translate to lower population growth than prior to wolf restoration.

In chapters 14, 15, and 16 we examine the age and sex characteristics, reproduction, survival, dispersal, and population growth rates of cougars before and during wolf restoration. In the final part of the book we synthesize the information and examine the niches of cougars and wolves and the implications of competition for management and conservation of cougars in multi-carnivore systems.



## CHAPTER 14

### Cougar Population Structure

Some of the most sought-after information in wildlife population biology is how many cougars reside in an area or specific habitat and the age distribution and sex ratio of those individuals. These are valuable pieces of information for helping to determine harvest regulations, for evaluating the effects of predation on prey, or for other human actions to manage and conserve the species (Mills 2007). Examining the numbers and age and sex structure of PW and DW cougars in our study was necessary to help us understand other population characteristics, including reproduction, survival, and turnover of individuals in the population through philopatry, immigration, and emigration. In combination, these characteristics helped us better understand the growth of each population during the period it was studied.

#### DETERMINING NUMBERS AND AGE AND SEX STRUCTURE

To monitor a large proportion of individuals in conjunction with providing the best estimates of the minimum number of cougars present, we intensively surveyed the study area during our capture work each winter (table 14.1). We sexed and aged individuals at capture, or we used known or estimated birth dates to determine ages of cougars during winter each year. When possible, kittens were sexed and aged at their natal den at 4.5 to 8.5 weeks of age (Murphy 1998; Logan and Sweanor 2001). Kittens not sexed and aged during this time frame were generally captured during the first winter after birth, when they were four to eight months of age (fig. 14.1). We describe many of these methods in detail in chapter 3. For cougars older than twelve months of age with unknown birth dates, we assumed a birth date of June 15 based on the primary birth peak of May through July for both study phases.

Unlike males, females showed selection for intermediate ranges of wolf use while using lower and higher wolf use areas less (see fig. 11.8d, tables 11.7, 11.8). Female cougars may have used density and intensity of wolf use as information on resource quality and costs of competition, as we discuss later.

We used estimated ages for each captured cougar to back-log them into the study population following methods of Logan and Sweanor (2001). Cougars that were thirty-six months of age or older at capture were likely to have entered the population as adults at some earlier date. Because we had probably missed them during previous years of capture, backlogging them into the population enabled us to account for their presence. After backlogging all known cougars, we then estimated the proportion of adults marked each year using percent accuracy methods of Logan and Sweanor (2001: 67). This gave us an indication of the percentage of the population we had radio-marked each year of the study.

During the PW study, an estimated 77 percent of adult cougars were radio-marked by winter 1988–89, with 87–94 percent radio-marked in all subsequent years until the final year of study. As wolves were restored, we radio-marked an estimated 68 percent and 88 percent of adult cougars present in the study area by winters 2000–2001 and 2001–2, respectively, with 88–93 percent radio-marked in all subsequent years until the final year of study (Ruth et al. 2011). Changes in cougar numbers appeared unrelated to survey effort, which increased only slightly between the PW and DW studies (Murphy 1998). The cougar population grew from an estimated average of 9.4 adult cougars in the PW study to an average of 16.6 adult cougars in the wolf restoration study—an approximately 76 percent increase in adults. We discuss in greater detail in chapter 16 the numbers of cougars each year, their density across the study area, and population growth.



**FIGURE 14.1.** To monitor numbers of cougars in the study area each winter, we attempted to sex and age all individuals. Kittens not sexed and aged at their natal den at 4.5 to 8.5 weeks of age were generally captured during the first winter after birth, when they were four to eight months of age, such as four-month-old male kitten M195. Photo by Jason Husseman, Hornocker Wildlife Institute/Wildlife Conservation Society.

In addition to our capture and marking methods, our long-term research provided an opportunity to explore two non-invasive genetic sampling methods that showed promise—hair snares and snow tracking (Mowat and Paetkau 2002; Frantz et al. 2004; Long et al. 2008). Our interest in these techniques led us to initiate a three-year study between 2003 and 2005 of our post-wolf restoration study. The project was a component of dissertation research conducted by Mike Sawaya (fig. 14.2a; see Sawaya et al. 2011).

The study confirmed that snow tracking yielded more hair and scat samples and was more cost-effective than attempting to snag hair using rub pads. Further, the sampling methods can provide a low-cost, long-term population monitoring alternative, reducing the need for capturing and collaring cougars, depending on conservation and management needs and objectives. We successfully backtracked to a hair sample 80 percent of the time when tracking condi-

tions were favorable (fig. 14.2b). Overall, backtracking in snow yielded DNA samples that enabled us to identify and sex accurately 22 (9 females, 13 males) of the 29 (15 females, 14 males) radio-collared adults, subadults, and kittens present on the study area during the combined winters of 2004 and 2005 (Sawaya et al. 2011). Over that two-year sampling period, we detected 12 of 14 (86 percent) adult individuals that were radio-located on the study area. We also identified some limitations of collecting samples along backtracking routes, including failure to detect 1 adult female and successfully amplifying DNA from 2 individuals after they had died (see Sawaya et al. 2011). Yellowstone National Park has shown interest in utilizing these methods to sample the cougar population occasionally within the park, and state agencies have since used backtracking methods, coupled with other non-invasive techniques, to monitor population trends in other areas (Russell et al. 2012).

**TABLE 14.1** Summary of cougar population monitoring efforts during wolf restoration on the Greater Yellowstone Northern Range, winters 1998–2005.

|                                  | 1998–99 | 1999–2000 | 2000–2001 | 2001–2  | 2002–3  | 2003–4  | 2004–5 <sup>a</sup> |
|----------------------------------|---------|-----------|-----------|---------|---------|---------|---------------------|
| Successful captures <sup>b</sup> | 16      | 16        | 18        | 15      | 14      | 21      | 7                   |
| Person-days of capture effort    | 162     | 167       | 171       | 168     | 170     | 206     | 142                 |
| Person-days per capture          | 10.8    | 10.4      | 9.5       | 11.2    | 12.1    | 9.8     | 20.3                |
| Kilometers of transect searched  | 1,589.1 | 1,208.7   | 1,621.3   | 1,556.8 | 1,226.9 | 1,197.1 | 826.5               |

<sup>a</sup> Capture and track survey efforts were reduced and concentrated to a portion of the study area to recapture and place GPS collars on selected adult and subadult cougars. Collars were removed from all individuals by 2006.

<sup>b</sup> Total successful captures.

## AGE STRUCTURE

Adult cougars typically make up the largest proportion of individuals in a population, followed by kittens and then subadults. The proportions we observed in our study were very similar to those described in two other studies (47–56 percent adults, 0–17 percent subadults, and 24–44 percent kittens; Logan and Sweanor 2001; Robinson and DeSimone 2011). Over the course of six PW years, the population consisted on average of 35 percent adult females, 13 percent adult males, 10 percent subadults, and 42 percent kittens (for adults, see fig. 14.3). These proportions changed little during wolf restoration, when there were on average 40 percent adult females, 13 percent adult males, 15 percent subadults, and 32 percent kittens in the population over six years [1]. The slight increase in the proportion of subadults and the drop in the proportion of kittens during wolf restoration resulted, we suspect, from kittens attaining independence from their mother at an older age—and females thus having a longer interval between births, as we discuss in chapter 13.

Prior to the arrival of wolves, the ages of adult male cougars and adult female cougars were similar across study years, with a median age of 45–62 months for males and 49–71 months for females [2]. These typically three- to six-year-old adults, reflecting recent restoration of immigrant and philopatric offspring, were similar to the young age structure of populations that are heavily exploited by humans (see Robinson and DeSimone 2011). Although PW females averaged 10–19 months older than PW males, this difference was not substantial (table 14.2) [3]. In contrast, DW males and females aged as the study progressed. However, occasional turnover of males resulted in little statistical difference in DW male ages, while DW females progressively grew older through the years of study (table 14.1) [4]. Females averaged 12–17 months older than males except in the final year of study, when eight females averaged 72 months older than

two recently established males on the study area [5]. When comparing the PW and DW studies, the average age of adult males was 12.5 months younger prior to wolves than during wolf restoration, and adult females were about 20 months younger. This age structure difference reflected newly establishing individuals and population growth prior to wolves as well as stable growth with an aging assemblage of adult cougars during wolf restoration [6]. Hence, in contrast to our predictions, there was little turnover of adults during wolf restoration, and cougars survived to relatively old ages within the boundary of Yellowstone National Park.

Unlike males, females showed selection for intermediate ranges of wolf use while using lower and higher wolf use areas less (see fig. 11.8d, tables 11.7, 11.8). Female cougars may have used density and intensity of wolf use as information on resource quality and costs of competition, as we discuss later.

The tendency for females to reach older ages than males within study phases was reflective of the overall greater survival rates for adult females. The oldest female in our study, F53, lived to 14.5 years old (174 months). Female F53 was captured as a 20- to 21-month-old subadult in April 1989 during the PW study. She established and remained as a resident adult. We recaptured her as we marked cougars during wolf restoration, and she survived until a deadly encounter with the Agate wolf pack in February 2004. Males that lived exclusively within the boundaries of Yellowstone did not typically live beyond 10 to 11 years of age.

In many studies of wild cougars, adult females have typically been found to survive longer and reach older ages than adult males (Hopkins 1989; Cunningham et al. 2001; Robinson and DeSimone 2011). Two notable exceptions to this pattern were documented in two areas where there was no human hunting. Residing in the San Andres Mountains within the White Sands Missile Range, New Mexico, an adult male lived to an estimated 12.7 years and an adult





**FIGURE 14.2.** Mike Sawaya backtracking a cougar to collect hair and scats during his non-invasive genetic sampling study (A). Backtracking cougars in snow proved to be an efficient, reliable method to collect hair from bed sites and natural hair snags such as branch tips and thorn bushes. Snow tracking yielded more hair samples and was more cost-effective than attempting to snag hair using rub pads (B). Hornocker Wildlife Institute/Wildlife Conservation Society photos.

female to an estimated 12.2 years (Logan and Sweanor 2001). In southern Florida a male cougar reached 15 years before he was killed by another male, and a female reached 13.2 years before she was killed by a vehicle (Maehr 1997a). In contrast to cougars reaching ages of 11 years and older when living in protected areas, populations that are heavily exploited by human hunting tend to be composed of relatively young cougars. Older adults, particularly males, are highly sought and are subsequently replaced by young immigrants or philopatric offspring (Logan and Sweanor 2001; Stoner et al. 2006; Quigley and Hornocker 2010; Newby et al. 2013).

## SEX STRUCTURE

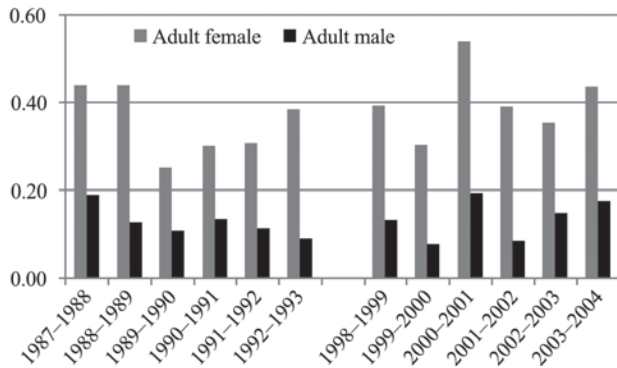
In most mammals the *primary* and *secondary sex ratios*, ratios at conception and at birth, respectively, typically do not differ from 1:1 males to females (Mills 2007). The *tertiary sex ratio* associated with puberty also may not differ from equality. In the polygamous and promiscuous mating system of

cougars, which is influenced by sexual selection and competition for mates, the *quaternary* sex ratios associated with breeding adults are typically skewed (Seidensticker et al. 1973; Anderson 1983; Logan and Sweanor 2001, 2010; Mills 2007: 84). Although sex ratios may change over time, adult male cougars are typically outnumbered by adult females.

## Kittens

Kittens were located in 29 dens during the PW study and marked at an average age of 4.5 weeks (range = 1–8 weeks) and at a mean age of 20.9 weeks (range = 10–52 weeks) of age after they had left the den (K. Murphy, unpubl. data). As wolves were restored in the study area, we successfully sexed, aged, and marked kittens at 24 dens at an average age of 5.6 weeks (range = 4.5–6.5 weeks) and at a mean age of 19.7 weeks (range = 9.5–54 weeks) of age after they had left the den. Thus we radio-collared 57–78 percent of kittens in the PW study and 60–70 percent of kittens in the DW study





**FIGURE 14.3.** Proportion of adult female and adult male cougars of the total minimum population estimate prior to wolf restoration (1987–93) and during wolf restoration (1998–2004) on the Greater Yellowstone Northern Range, Montana and Wyoming.

prior to 3.5–4.8 months of age (fig. 14.4a, 14.4b; Ruth et al. 2011). Over the course of the PW study, 1–12 female and 1–14 male kittens were monitored each year. We were similarly able to monitor 0–9 female and 0–10 male kittens during wolf presence (Ruth et al. 2011) [7]. While female kittens were monitored over similar lengths of time between study phases, we monitored DW male kittens longer than PW male kittens, primarily because more were available [8].

For cougar litters where we were able to count and sex the entire litter at 8 weeks of age, we found that the sex ratio of 14 nursing litters was somewhat female skewed, with 21 females and 15 males—resulting in a male:female ratio of 1:1.4 in the PW period. By contrast, the sex ratio was somewhat male skewed during wolf restoration. We documented 21 males and 15 females in 13 nursing litters, resulting in a male:female ratio of 1:0.7. As with adults, neither of these secondary sex ratios differed from a 1:1 ratio, and the differing skew in sex ratios between study periods was not statistically significant [9]. When we looked over a longer time frame by combining study phases, the sex ratio was exactly equal—36 male and 36 female kittens.

Several studies have documented fairly equal litter sex ratios (Seidensticker et al. 1973; Pierce and Bleich 2003; Lambert et al. 2006). In three of the studies there were more females than males (Logan et al. 1986; Ross and Jalkotzy 1992; Lambert et al. 2006), while two other studies reported more males than females (Ashman et al. 1983; Spreadbury et al. 1996)—although none of the ratios differed from equality. Information from most of these wild populations represented a wide range of kitten ages, whereby postnatal mortality may

**TABLE 14.2.** Sex ratios and mean ages of adult cougars prior to presence of wolves (1987–93) and during wolf restoration (1998–2005) on the Greater Yellowstone Northern Range, Montana and Wyoming.

| Study Phase<br>and Year | Sex<br>Ratio <sup>a</sup> | Male Ages (months) <sup>b</sup> |      |      | Female Ages<br>(months) <sup>b</sup> |       |      |
|-------------------------|---------------------------|---------------------------------|------|------|--------------------------------------|-------|------|
|                         |                           | N                               | Mean | SD   | N                                    | Mean  | SD   |
| PRE-WOLF                | M:F                       |                                 |      |      |                                      |       |      |
| 1987–88                 | 1:2.3                     | 2                               | 46.9 | 8.6  | 6                                    | 65.7  | 25.1 |
| 1988–89                 | 1:3.5                     | 3                               | 49.4 | 3.8  | 9                                    | 65.6  | 26.2 |
| 1989–90                 | 1:2.3                     | 2                               | 62.3 | 4.2  | 10                                   | 60.0  | 30.3 |
| 1990–91                 | 1:2.3                     | 4                               | 51.4 | 23.4 | 9                                    | 64.2  | 35.5 |
| 1991–92                 | 1:2.8                     | 5                               | 56.3 | 25.3 | 11                                   | 66.5  | 37.6 |
| 1992–93                 | 1:4.3                     | 6                               | 58.4 | 31.1 | 10                                   | 68.3  | 36.6 |
| 1993–94                 | —                         | 6                               | 53.6 | 28.3 | 4                                    | 65.3  | 13.1 |
| Average all years       | 1:2.9                     |                                 | 54.5 | 22.5 |                                      | 65.0  | 30.5 |
| DURING WOLF             | M:F                       | N                               | Mean | SD   | N                                    | Mean  | SD   |
| 1998–99                 | 1:3.0                     | —                               | —    | —    | 4                                    | 56.7  | 11.6 |
| 1999–2000               | 1:4.0                     | 2                               | 78.1 | 26.1 | 5                                    | 69.4  | 10.0 |
| 2000–2001               | 1:2.8                     | 5                               | 57.0 | 30.2 | 11                                   | 74.0  | 32.7 |
| 2001–2                  | 1:4.7                     | 3                               | 67.9 | 35.0 | 14                                   | 84.2  | 40.1 |
| 2002–3                  | 1:2.4                     | 4                               | 71.4 | 32.2 | 14                                   | 86.5  | 33.6 |
| 2003–4                  | 1:2.5                     | 4                               | 85.3 | 27.3 | 11                                   | 97.5  | 32.0 |
| 2004–5                  | —                         | 2                               | 34.8 | 5.2  | 8                                    | 106.2 | 20.7 |
| Average all years       | 1:3.2                     |                                 | 67.0 | 29.4 |                                      | 85.1  | 32.9 |

<sup>a</sup> Sex ratios were determined from the number in each sex class based on the minimum estimated number of adult females and males at the end of winter each year.

<sup>b</sup> See chapter 3 for how we determined ages of cougars.

have affected observed sex ratios (Logan and Sweanor 2001). The shorter length of many studies may also have limited the information available, as longer studies like ours and Logan and Sweanor's (2001) found skewed sex ratios of litters examined at less than 8 weeks of age. Thompson (2009) more recently reported male-skewed (5:1) sex ratios of cougar litters in the Black Hills of South Dakota.

### Subadults

Subadults make up the smallest proportion of cougar populations because they usually emigrate or leave their natal area, and their mortality rates may be high during this time (Logan and Sweanor 2001). These characteristics also made it difficult to gather survival information and establishment rates for this age group. There were few subadults present each year in the study area, so we combined years. As with adults and kittens, *tertiary* sex ratios were not different from

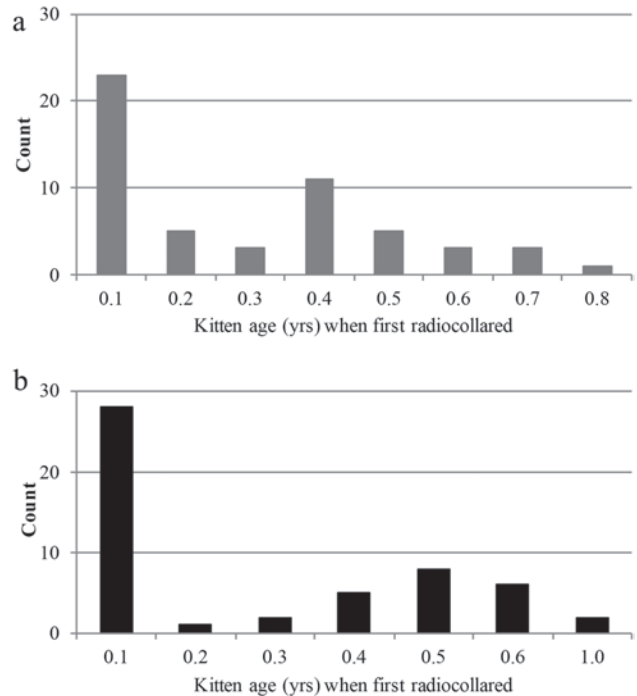
1:1, and when we looked over a longer time frame by combining study phases, the sex ratio was exactly equal—22 males and 22 female subadults [10]. Yet prior to wolf restoration, the ratio was skewed toward females outnumbering male subadults (1:2.4), and during wolf restoration it was skewed toward males outnumbering females (1:0.59), which represented clear differences between the two study periods [11]. This skewed pattern in each study phase was similar to the skewed sex ratios we observed for kittens.

### Adult Cougars

On the Greater Yellowstone Northern Range, adult female cougars outnumbered adult males at similar ratios before and during wolf restoration, although the number of females each male overlapped increased after wolf restoration (table 14.2). When we averaged across all years, there were roughly 3 adult males to 9 adult females, for a mean sex ratio of 1:2.9 prior to wolf restoration. During wolf restoration, there were on average 4 males to 12 females, for a mean sex ratio of 1:3.2 across all years. These mean ratios were similar between study phases and did not differ from a hypothetical 1:1 male to female sex ratio [12]. Annually, the ratio of adult males to adult females also did not differ from a hypothetical 1:1 sex ratio except near the end of the PW study and in 1999–2000 and 2001–2 of the DW study, when females outnumbered males 4 to 1 (table 14.2) [13]. There might be numerous explanations for why females significantly outnumbered males during these years, including more rapid settlement of females during population increases and the higher turnover of males as related to their shorter lifespan. Our findings mirror those of other studies that documented fairly equal adult sex ratios and suggest that in most years, losses of an adult from one or the other sex are replaced in kind (Seidensticker et al. 1973; Logan and Sweanor 2001: 73; Lambert et al. 2006; Quigley and Hornocker 2010).

### ADAPTIVE EXPLANATIONS OF SEX-RATIO VARIATION

Numerous hypotheses have been proposed to provide an adaptive explanation of sex-ratio variation observed in mammals and birds (Emlen 1997; Cockburn et al. 2002). Most of the hypotheses focus on the idea that parents should adjust the sex ratio of offspring in response to factors that affect their own and their offsprings' future survival and reproductive success (Clutton-Brock et al. 1984). Although selection



**FIGURE 14.4.** Distribution of ages when kittens were first radio-collared prior to wolves (a;  $n = 54$  kittens) and during wolf restoration (b) on the Greater Yellowstone Northern Range. Kittens radio-collared earlier than 3.5–4.8 months of age amounted to 57–78 percent of kittens before wolves and 60–70 percent during wolf restoration. No kittens less than four weeks old were radio-collared.

should favor equal primary sex ratios under most conditions, secondary sex ratios are frequently found to be skewed (Trivers and Willard 1973; Cockburn et al. 2002).

What might best explain the skewed secondary sex ratios we observed after the arrival of wolves as compared to the PW study period? One hypothesis posits that females in better physical condition—with more access to resources—should produce more offspring of the sex that would most benefit from the mother's improved condition (Trivers and Willard 1973; Mills 2007: 84). For example, in the polygynous cougar system, where males compete and hypothetically mate the most, mothers might invest more in male offspring when food resources are plentiful, thus increasing their reproductive success as well as hers. In New Mexico, Logan and Sweanor (2001) found that young females producing first litters—and thus at a smaller maternal body mass—had sex ratios biased toward females and were investing in less costly female offspring (also of smaller body

mass). In subsequent litters, more males were born. Older, full-grown, and thus larger and more experienced mothers were able to invest more in male offspring. This explanation also seems plausible for our observations. In the PW study, the sex ratio skewed toward female cougars was consistent with a younger age structure of females and a greater number of first-time litters. Older, more experienced mothers during wolf restoration invested in male offspring. We had few data to examine this hypothesis fully. Prior to wolf restoration, five of six first-time mothers produced litters biased toward females—five male and nine female kittens. Two philopatric females had not yet produced first litters by the end of the PW study. During wolf restoration, three first-time mothers produced a total of three male and two female kittens.

A more recent analysis leans more heavily on habitat quality and sex-biased dispersal as the greater determinants of sex ratio at birth, also known as the local resource competition (LRC) hypothesis (Clark 1978; Taylor 1994; Julliard 2000). In heterogeneous environments, in which some habitats are more favorable to reproduction than others, an individual should attempt to increase the number of offspring establishing in high-quality habitats. Hence biases in offspring sex ratio should tend toward the more philopatric sex in good-quality habitats and toward the more dispersing sex in poor-quality habitats. The quality of a local habitat may be constrained by abundance of resources and intra- and interspecific competition for those resources—including mates. In many mammals where males are the main dispersing sex and females are more philopatric, as in cougars, mothers in poor habitat and body condition are predicted to produce more sons that should disperse, on average, while those in good condition are predicted to produce more daughters (Hewison et al. 1999).

Based on our observations in the two study phases, this latter hypothesis seems reasonable. Prior to wolf presence, elk were abundant, their numbers were increasing, and elk distribution varied across the study area, as did the habitats that provided cover for cougar hunting and security. At this time, when cougars were increasing on the Greater Yellowstone Northern Range, areas in which cougars could establish home ranges were available. At least six female kittens born in the study area were philopatric, establishing home ranges near or adjacent to those of the mothers (see chapter 15; Murphy 1998). By investing more in female offspring during good habitat conditions prior to wolves, a female cougar could increase her inclusive fitness as well as that of her mates.

During wolf restoration and in conjunction with the declining elk population, wolf and bear numbers increased, and cougars strongly avoided areas of high wolf use. In doing so, a greater number of cougars overlapped in habitat that provided high-quality escape cover, but these areas generally held a lower abundance of elk. Except on occasion, there was less room for subadults to establish in the study area during wolf restoration as compared to the PW study period. Greater competition for fewer resources and fewer territories for establishment can be viewed as poor-quality habitat conditions. Producing more offspring of the more dispersing sex—male cougars—in low-quality habitat conditions would enhance dispersal into potentially higher-quality habitats farther away (Julliard 2000).

The nutritional sex-bias hypothesis and the habitat quality dispersal hypotheses could be intertwined. During the years Logan and Sweanor (2001) followed desert cougars, their study area experienced several years of drought in the later study years. While they do not report the sex ratio of kittens in the early phase of their study when conditions were good compared to the sex ratio of kittens produced during the period of drought, these good and poor conditions perhaps also influenced the observed sex ratio of kittens in their study area. Examining the production of litters in poor-quality habitats versus high-quality habitats across the Greater Yellowstone Northern Range with individuals as the sample unit could yield insights. Yet a realistic constraint is that some females may quickly lose litters in poor-quality resource conditions, and we noticed a lack of reproductive output associated with the Grand Canyon of the Yellowstone in the DW study (see text box 14.1). Hence sex ratios in periods of poor quality may be underrepresented because of lost litters. We follow up on the role of resource conditions in chapter 16 when we examine why mothers supported offspring longer during wolf presence and the adaptive significance of dispersing versus staying.

## SUMMARY

We estimated numbers of cougars residing in the study area and documented sex and age structure each year using capture-mark-and-recapture and radio-telemetry techniques. After adding in cougars we apparently missed in previous years through backlogging, we accounted for 87 percent to 94 percent of the minimum number of adult and independent subadult cougars present at the time of the PW and DW studies. We also evaluated the effectiveness of hair snag pads and

backtracking to collect genetic samples and concluded that these methods proved useful for monitoring cougar numbers and sex ratios. We detected 86 percent of adult cougars within the study area by backtracking in snow to collect genetic samples, thus proving this method to be an efficient, reliable, non-invasive sampling technique for cougars in areas with snow.

As in many other studies, adult male cougars were outnumbered by adult females roughly three to one as a result of the social and mating behavior of adult cougars. During both study periods, the cougar population consisted of 48–53 percent adults, 10–15 percent subadults, and 32–42 percent kittens. The age structure of cougars differed between the PW and DW study periods, reflecting younger, newly establishing adults prior to wolf restoration and an aging assemblage of adult cougars during wolf restoration. Adult females

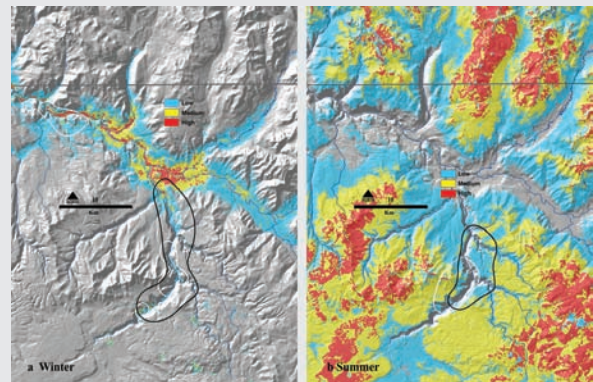
lived relatively long lives during wolf restoration, with one female surviving to 14.5 years old. The sex ratio of kittens at less than 8 weeks of age was biased toward female kittens in the PW study phase and toward male kittens during wolf restoration. As elk were abundant and carnivore competitors were few prior to wolf restoration—conditions that reflect good-quality habitat—females producing more female offspring increased their fitness because their female offspring remained in the good-quality habitat. Our findings could be explained by two potentially interacting hypotheses. Yet we felt our data best fit the hypothesis that biases in offspring sex ratio tend toward the more philopatric sex in good-quality habitats (i.e., cougar females in the PW study) and toward the more dispersing sex in poor-quality habitats (i.e., cougar males during wolf restoration).

#### Text Box 14.1. Why No Kittens?

During wolf restoration, three females resided along the Grand Canyon of the Yellowstone between Tower Junction and Broad Creek. First-time mother F120 and mature female F123 apparently had three failed litters between 2002 and 2003. On two occasions F120 localized for four to five weeks but then began making substantially large movements, and we confirmed that she did not have kittens with her. Wedged between but separate from these two events, F120 bred with male M148, yet we did not find that she localized, and subsequent tracking and sightings revealed no kittens. In May 2004 F120 produced and successfully reared two kittens while residing in the same home range. Upon capture in February 2001, eight-year-old female F123 was accompanied by one male and one female kitten that eventually dispersed from the study area by summer 2002. Similar to female F120, female F123 localized for four to five weeks—indicating denning behavior—but she then began making large movements, and subsequent tracking and sighting revealed no kittens. Wedged between these two events, F123 consorted with male M127, but she did not localize, and no kittens were seen while we continued to follow her. She did not produce any offspring through June 2005, when she was about eleven years old and her collar fell away. A third female, F53, born and established during the PW period, was accompanied by a single kitten in 2001. She also did not produce a litter of kittens from 2002 through February 2004, when she was killed by the Agate wolf pack.

These females overlapped with one to two males that successfully sired offspring with other females, so what might explain the lack of reproductive output in this part of the study area? All three females overlapped with the Agate and Specimen Creek wolf packs but mostly during winter, when

none of these females exhibited denning behavior. Female F53 may not have reared more offspring because of advanced age of thirteen years; her death was at fourteen years of age. The area in which they resided was a favorite spring and early summer foraging zone for grizzly bears, and the park restricted human travel into the area during the time of greatest bear activity. Other females, such as female F125, were more greatly overlapped with wolves and were frequently displaced by bears but were highly productive. Availability of prey may have played a role, as shown in figure 14.5, but ultimately we did not have a clear answer.



**FIGURE 14.5.** Winter (left) and summer (right) home ranges (95 percent fixed kernel) of female cougars F123 (white) and F120 (black) along the Grand Canyon of the Yellowstone, Yellowstone National Park. Elk use, predicted from a resource selection function (Mao et al. 2005), is shown as categories of low (blue) medium (yellow), and high (red) probability of use.



## CHAPTER 15

### Reproduction and Survival Rates of Cougars

#### CONTRIBUTING AUTHORS

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Selected genetic traits that maximize individual reproductive success and survival are key components of cougar population persistence (Logan and Sweanor 2010). Traits that enhance survival, such as increased awareness of threats or physical abilities that enable an individual consistently to escape competitors and other hazards, may then be passed on to multiple generations of offspring via reproductive success (Murray and Patterson 2006: 1499). Hence those individuals that live longer lives are the ones that have more opportunities to breed and produce offspring (Murphy 1998; Logan and Sweanor 2001).

We documented reproduction and survival over a total of fourteen years—seven years prior to wolf restoration and seven years after wolves were restored; few other cougar population studies have been as extended (but see Logan and Sweanor 2001). In this chapter we first examine whether breeding, birth, and lactation chronology differed between the PW and DW studies and whether mean litter size and overall fecundity changed after wolf restoration. We then assess causes of mortality and factors that explain survival rates for cougars, as set forth with our hypotheses and predictions in chapter 13.

#### TIMING OF MATING

In contrast to wolves, in which the alpha pair mates in February each year, cougars may mate at any time of the year. Yet in most systems, a peak in cougar breeding typically occurs corresponding with late winter, spring, and early summer—and this peak is most pronounced in northern latitudes (Ross and Jalkotzy 1992; Murphy et al. 1999; Logan and Sweanor 2001).

As we followed cougars throughout the year, we documented scent-marking behavior by adult males, subadult

males, and adult females. Dominant males scraped throughout their home ranges to reduce the degree of trespass by other males (both residents and new immigrants) and to check on the status of each female in their home range—as the reproductive status of females changed because of loss of kittens. In our study area, males recently independent of their mothers and new immigrant males were spatially restricted to winter range, where they spent their first winter overlapped with resident males. Although scraping may be risky behavior, while sampling subadult males during our kill rate sequences, we observed variation in behavior with respect to movements and scent-marking with scrapes. One subadult male maintained a low profile while others scraped frequently (see text box 15.1). These contrasting behaviors suggested more venturesome behaviors from some individuals in testing an area and opportunity to mate, which may also be hormonally driven, whereas others may bide their time to disperse and establish elsewhere.

Although our data were sparse on the timing of scraping by all solitary females, we did observe this scent-marking behavior by a few solitary females when they were in estrus. Because urine accurately reflects the level of estrogen in the bloodstream, with increased estrogen levels occurring during the estrous cycle (Gorman and Trowbridge 1989), our observations support the notion that females scrape to advertise their reproductive status to potential mates—a finding similar to that for female tigers, which apparently scent-marked most intensively at the onset of estrus (Smith et al. 1989).

Once they connected via scent-marking, a male and female cougar spent anywhere from one to sixteen days together for breeding, with numerous copulations occurring during this time (Seidensticker et al. 1973; Anderson

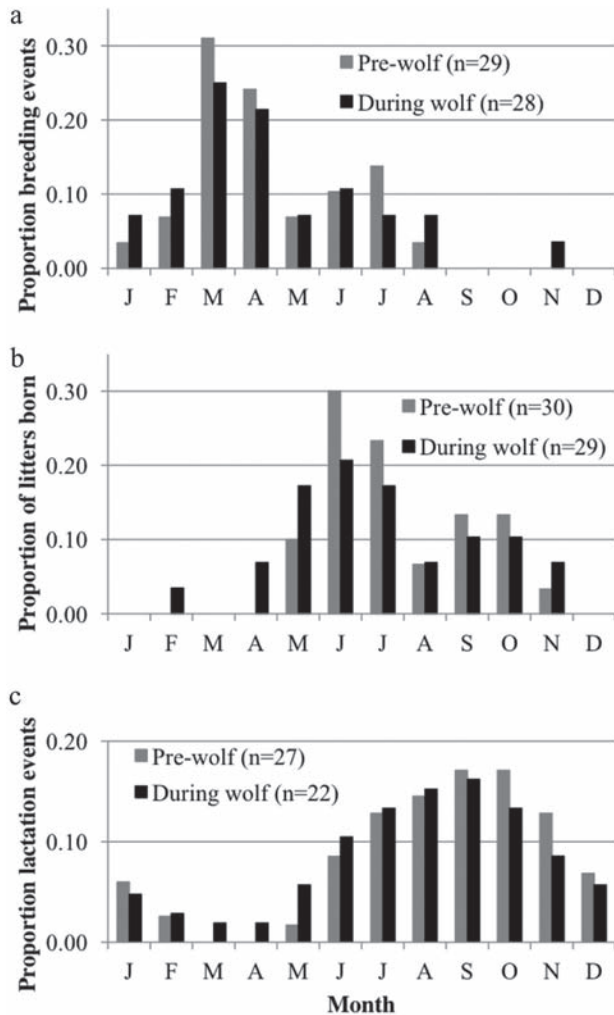


**FIGURE 15.1.** Female F106 (foreground) and M137 (against cliff) during a breeding association below the cliffs of Mount Everts, Yellowstone National Park, January 2001. Photo by Polly Buotte, Hornocker Wildlife Institute/Wildlife Conservation Society.

1983; Beier et al. 1995; Logan and Sweanor 2000). Females may eventually produce multiple litters with the same male, but they sometimes mate with more than one male in individual or consecutive estrous cycles (Young and Goldman 1946; Logan and Sweanor 2000, 2001). We made one such observation of a female mating with multiple males as we conducted kill rate sampling from January 5 through March 13, 2001 (see text box 15.2; fig. 15.1). Such promiscuity may have evolved as a means by which females assess male vigor and thus may contribute to a female's reproductive success (Eaton 1976; Logan and Sweanor 2010). Promiscuity also might allow a female to establish positive relationships with all the males that share or abut her home range, confusing paternity among male mates and perhaps reducing instances of infanticide and aggression toward the female in subsequent encounters (Logan and Sweanor 2000, 2010). Although females may spend time with multiple males during mating, residency and dominance provide strong fitness benefits to tenured males (Murphy 1998). Greater

Yellowstone Northern Range females typically showed strong fidelity to the same males during breeding from year to year.

Our intensive monitoring of radio-collared adults allowed us to document 57 breeding associations as well as birth chronology for 30 reproductive events for 15 PW females and 29 reproductive events for 14 females during wolf restoration. When we lacked observation of a male-female breeding association prior to documenting the birth of a litter, we determined the date of conception using mean gestation in the following manner: date of conception equaled the Julian birth date minus a 91-day mean gestation. Birth dates of kittens were estimated from the first date when radio-telemetry locations indicated site fidelity of the adult female for greater than 2 weeks. We also used the average gestation length of 91 days to predict birth dates of litters from documented associations of males and females. We noted these dates on a calendar and kept on the lookout for localization of movements by a female as the date approached.



**FIGURE 15.2.** Proportion of breeding events (a), litters born (b), and lactation (c) during each month for cougars prior to wolves (1987–94) and during wolf restoration (1998–2005) on the Greater Yellowstone Northern Range.

Although calf to cow elk ratios declined and cougars altered their use of the landscape and avoided wolves, their social structure was not less stable than in the PW period, and we found few changes in breeding or birth chronology as wolves recolonized the study area. The timing of peak breeding in late winter—when males and females were overlapped on winter range—remained consistent, with peak breeding occurring mostly in late March through April (fig. 15.2a). A smaller secondary peak in breeding occurred during May, June, and July.



**FIGURE 15.3.** These three six-week-old kittens of female F107 are peering from their den in a rock crevice below cliffs near Abiathar Peak, Yellowstone National Park. Photo by Toni Ruth, Hornocker Wildlife Institute/Wildlife Conservation Society.

### TIMING OF BIRTHS

Timing of births during the two studies had a pattern similar to that of breeding but delayed by the three months of gestation (fig. 15.2b). Kittens were born in dens—located in boulder jumbles and amid rock outcrop with dense vegetation or downed trees—primarily during two noticeable birth peaks (fig. 15.3). Of 59 litters, 35 (59 percent) were born during a peak birth period in May, June, and July (fig. 15.2b). Another 18 litters (31 percent) were born during a secondary, less pronounced birth peak occurring in August, September, and October in both study phases. Where birth month could be confirmed, 10 percent of litters were born outside the May through October period, with only 1 litter born in February and 2 in April.

The occurrence of litters during the primary birth peak was greater than expected from a uniform distribution and coincided with the birth of primary prey, elk calves and deer fawns, which also occurred in late May through early July [1]. Like deer fawns, elk calves may have been selected by cougar mothers both because they were more abundant in spring and summer than at other times of the year and because they were a vulnerable component of the elk population extending into winter (chapter 7; Pierce et al. 2000a). Access to abundant, easily catchable prey—including small mammals—would appear to set mothers up to be able to support offspring through the increased



energetic demands of lactation, of feeding offspring as they become more mobile away from the den, and of harsh winter conditions.

We searched the literature for data on the maximum lactation period of cougars to calculate lactation chronology. Literature suggested that lactation in female cougars lasted a maximum of 60–120 days for captive (60–90 days, Eaton and Velandier 1977) and wild cougars (90–120 days, Hemker et al. 1986). Because the literature revealed no visual observations of maximum lactation or nursing in wild cougars, we used data from a single visual observation of 118-day-old kittens nursing for approximately 20–30 minutes. We calculated lactation chronology as the Julian birth date plus a maximum lactation of 118 days for 27 litters prior to wolves and 22 litters during wolf presence. Figure 15.2c shows the distribution of months in which females were lactating on the Greater Yellowstone Northern Range. Although they were still supporting dependent offspring, fewer females were lactating during winter months. This finding has important implications for hunting regulations, which usually state that a female with kittens by her side or one that is lactating may not be harvested. In the final chapter of this book we discuss harvest seasons relative to the breeding, birth, and lactation chronology of our mostly non-hunted population.

The fact that some cougars bred and produced kittens outside the primary birth peak (the time frame that appears most advantageous for food acquisition) may be explained partly by loss of litters during the birth peak, dispersal of kittens in spring, and the fact that cougars are polyestrous, cycling into reproductive receptivity continually throughout the year (Bonney et al. 1981; Logan and Sweanor 2001). Multiple estrous periods enable opportunities to conceive quickly and rear a second litter if the first litter is lost (Kleiman and Eisenberg 1973; Seidensticker et al. 1973). Because kittens experience higher mortality within the first 4 months of life, females that lost entire litters could quickly conceive again and give birth in 3 months' time (Hornocker 1970; Logan and Sweanor 2000). But we found wide variation in how quickly females bred again. Female cougars that lost entire litters within 18 to 169 days of birth (PW = 5 litters, DW = 6 litters) bred again within 7 to 277 days (average of 128.3 days).

In our DW study, closer examination suggested that giving birth in the secondary birth peak was more closely tied to dispersal. In nine of thirteen breeding events associated with the secondary birth peak, mothers bred close to the time

of independence of their yearling offspring—just prior to this (5 litters) or just afterward (4 litters). Although we were unable to determine the exact dates when offspring became independent, our estimates indicated that females bred with a male an average of 35 days before or after their yearling offspring became independent. For the remaining four of the thirteen breeding events, we either had no information on prior litters ( $n = 2$ ) or the breeding was not associated with dispersal of a previous litter ( $n = 2$ ).

Other northern cougar studies more typically report a single birth peak across the months of July through October, with fewer births outside this peak but some in almost every month of the year (Ross and Jalkotzy 1992; Robinson and DeSimone 2011). These studies provide data from more heavily hunted populations, where males and females are usually killed prior to and during peak breeding—with hunting often subsiding in April after seasons have ended or quotas are already filled. Although sample sizes are rather small for comparison, we suspect that the removal of adults could explain peak births skewed to slightly later months following a resorting of survivors and with breeding occurring later than what might be typical based on data from primarily non-hunted populations in northern latitudes. More information is needed to compare breeding and birth chronology in hunted and non-hunted populations for northern latitudes separately from southern latitudes. Females' ability to conceive quickly means that losses appear to be rapidly replaced, yet more information is needed to understand if, as among ungulates, late-born offspring have lower survival through winter than those that are born earlier (Clutton-Brock et al. 1987; Noyes et al. 2002). Timing of human hunting may also influence kitten survival via orphaning and increased infanticide that results from loss of resident adult males, as reported in other studies (Cooley et al. 2009; Packer et al. 2009; Robinson and DeSimone 2011).

## LITTER SIZE

In the PW study we documented the birth of 80 kittens from 30 litters produced by 15 of 16 marked female cougars (Murphy 1998). Of those kittens, 59 were ear-tagged and 54 were radio-collared in 24 of the litters. During wolf restoration we documented 74 kittens from 31 litters produced by 14 of 16 marked females. We ear-tagged and radio-collared 52 kittens in 24 of those litters. Females rarely moved den locations, even after we entered to examine a litter while the



mother was away. Kittens remained at nursery dens for eight to ten weeks, during which time mothers usually attended the nursing kittens on a daily basis except when out hunting. In June 2005 we confirmed an additional litter when we discovered that female F47 was pregnant with 3 full-term kittens (2 female and 1 male) at the time of her death from plague (*Yersinia pestis*).

Nursing litters were composed of 2 to 4 kittens, falling within the span of 1 to 6 reported for cougars across their range (Logan and Sweanor 2001) [2]. When we counted kittens at four to eight weeks of age, mean litter size of  $2.9 \pm 0.8$  (SD) in 14 litters during the wolf restoration period was the same as mean litter size of  $2.8 \pm 0.7$  (SD) in 16 nursing litters in the PW study [3]. For 24 litters observed at greater than nine weeks of age, mean litter size was  $2.5 \pm 0.8$  prior to wolves (14 litters) and  $2.0 \pm 0.6$  (10 litters) during wolf restoration [4]. The smaller litter sizes at greater than nine weeks of age in both study periods reflect mortality associated with increased exposure to various hazards as the mother moved the kittens away from the den to their first meals of meat (Logan and Sweanor 2001).

On the Greater Yellowstone Northern Range, long-lived females each produced between 3 and 5 litters—producing totals of 6 to 15 kittens per female—during the seven years we documented their reproduction in each study phase. The probability of producing litters of 1, 2, 3, and 4 kittens was overall not different between study phases [5]. However, prior to wolf presence, mothers had a somewhat greater probability of producing litters consisting of 3 kittens (0.48 versus 0.25) and a slightly lesser probability of producing a litter of 2 kittens (0.40 versus 0.54) than did females during wolf restoration.

Because females solely endured the energetic costs of gestation, lactation, and providing for their growing offspring, the ability to produce 2 to 3 kittens may be influenced by available resources to some degree. Yet our growing understanding from long-term research suggests little variation in litter size unless perhaps in extremes of limited food (table 15.1). Two studies that document litters at early ages (typically less than eight to nine weeks old) report litter sizes similar to those we found. Logan and Sweanor (2001) found a mean litter size of  $3.0 \pm 0.7$  for 53 litters in New Mexico, and Robinson and DeSimone (2011) documented a mean litter size of 2.9 (95 percent confidence interval = 2.7 to 3.1) for 24 litters in Montana. The latter study found that litter size was

not affected by hunting. Wilson and colleagues (2004) documented the lowest mean litter size (1.9,  $n = 14$ ) and suggested that the small litters were the result of limited food resources, but litters were apparently observed after becoming mobile away from the den. Although we do not think elk became a limiting resource during our study, the similar litter sizes we documented during high and lower elk abundance as well as lower and greater carnivore densities support Schaller's (1972: 179) hypothesis that litter size is not affected much by variations in food abundance. The continued survival of kittens past eight to nine weeks, however, was influenced by the availability of young of year ungulates, human hunting, and intra- and interspecific aggression (Robinson and DeSimone 2011; Ruth et al. 2011).

### PROPORTION OF BREEDING FEMALES AND BIRTH INTERVALS

The proportion of maternal and solitary females varied each year (table 15.2). On average, 69 percent (range = 40–88 percent) of radio-marked resident females produced new litters each year, and 72 percent (range = 40–100 percent) supported dependent offspring—those less than 18 months of age—each year during the PW study. During wolf restoration an average of 43 percent (range = 18–71 percent) of marked female cougars supported new litters of kittens each year, and an average of 76 percent (range = 54–100 percent) supported dependent offspring. Female cougars residing on the Northern Range were solitary and without dependent young for 18 percent to 35 percent (95 percent confidence interval) of their reproductive lives. Female cougars supported dependent young for 65–82 percent of their reproductive lives (calculations based on a 9.5-year reproductive life assuming survival to 13 years of age). The proportion of females supporting offspring on the Greater Yellowstone Northern Range was very consistent with adult females in other parts of North America. In the Garnet Range of Montana, 58 percent of females gave birth each year, and 89 percent were traveling with dependent young (Robinson and DeSimone 2011). In New Mexico's Chihuahuan Desert,  $52 \pm 18$  percent of resident females gave birth each year, and about 26 percent were non-producing adult females; in the Bighorn Mountains of Wyoming, 55 percent and 86 percent of adult females raised kittens during two consecutive winters (Logan 1983; Logan and Sweanor 2001).

**TABLE 15.1.** Mean litter sizes, sex ratios, and survival rates ( $\pm$  SD unless noted otherwise) for Greater Yellowstone Northern Range cougars compared to those in other cougar studies in North America.

| Hunting Status    | Mean Litter Size $\pm$ SD                  | M:F Ratio of Litters | Survival                                        |                      |                      |                      |                              |                      | Study                                   |
|-------------------|--------------------------------------------|----------------------|-------------------------------------------------|----------------------|----------------------|----------------------|------------------------------|----------------------|-----------------------------------------|
|                   |                                            |                      | Adult Females                                   | Adult Males          | Yearling Females     | Yearling Males       | Kitten Females               | Kitten Males         |                                         |
| None to light     | 2.9 $\pm$ 0.8                              | 1:1.40<br>(36 kits)  | 0.89 <sup>a</sup><br>(0.52, 1.00)               | 0.74<br>(0.13, 1.00) | 0.83<br>(0.80, 0.86) | 0.67<br>(0.54, 0.79) | 0.48<br>(0.43, 0.49)         | 0.45<br>(0.41, 0.49) | Pre-wolf (Murphy 1998)                  |
| None to light     | 2.8 $\pm$ 0.7                              | 1:0.71<br>(36 kits)  | 0.86 <sup>a</sup><br>(0.26, 1.00)               | 0.69<br>(0.01, 1.00) | 0.80<br>(0.70, 0.88) | 0.61<br>(0.33, 0.89) | 0.60<br>(0.56, 0.64)         | 0.58<br>(0.44, 0.71) | During wolf                             |
| Heavy             | 2.5 $\pm$ 1.0<br>(15 litters)              | 1:1.13<br>(17 kits)  | 0.77                                            | 0.33                 | 0.32                 | 0.37                 | 0.57 <sup>b</sup>            |                      | Lambert et al. 2006                     |
| None              | 3.0 $\pm$ 0.7<br>(53 litters) <sup>c</sup> | 1:0.97<br>(148 kits) | 0.52–1.0                                        | 0.61–1.0             | 0.88 <sup>c</sup>    | 0.56 <sup>c</sup>    | 0.63 <sup>c</sup>            |                      | Reference area (Logan and Sweanor 2001) |
| Simulated hunting | See above                                  | See above            |                                                 |                      | See above            | See above            | 0.59 <sup>c</sup>            |                      | Treatment area (Logan and Sweanor 2001) |
| Light             | 2.5 $\pm$ 0.8<br>(15 litters)              |                      | 0.87 $\pm$ 0.07                                 | 0.64 $\pm$ 0.11      | 0.76 $\pm$ 0.21      | 0.51 $\pm$ 0.24      | 0.72 $\pm$ 0.24              | 0.53 $\pm$ 0.17      | Cooley et al. 2009                      |
| Heavy             |                                            |                      | 0.73 $\pm$ 0.13 <sup>d</sup><br>0.67 $\pm$ 0.19 | 0.34 $\pm$ 0.21      | 0.59 $\pm$ 0.31      | 0.63 $\pm$ 0.29      | 0.59 $\pm$ 0.21 <sup>b</sup> |                      | Robinson et al. 2009                    |
| Heavy             |                                            |                      | 0.64 $\pm$ 0.07 <sup>e</sup>                    |                      |                      |                      |                              |                      | Stoner et al. 2006                      |
| Light             |                                            | 1:1 (18 kits)        | 0.76 $\pm$ 0.04 <sup>e</sup>                    |                      |                      |                      |                              |                      | Stoner et al. 2006                      |
| Hunted            | 2.9 $\pm$ 0.22 <sup>a</sup>                |                      | 0.67 $\pm$ 0.09                                 | 0.72 $\pm$ 0.14      | 0.49 $\pm$ 0.16      | 0.39 $\pm$ 0.16      | 0.78 $\pm$ 0.10              | 0.77 $\pm$ 0.11      | Robinson and DeSimone 2011              |
| None to light     | See above                                  |                      | 0.97 $\pm$ 0.03                                 | 0.78 $\pm$ 0.15      | 1.0                  | 1.0                  | 0.97 $\pm$ 0.04              | 0.67 $\pm$ 0.13      | Robinson and DeSimone 2011              |

<sup>a</sup> The variation is the 95 percent confidence interval instead of SD.<sup>b</sup> Survival rate is for all kittens—females and males combined.<sup>c</sup> Litter size based on all litters observed at <49 days in the combined reference and treatment study areas. Survival rates for sixteen females and nine males from independence to adult status or death were not separated between reference and treatment areas. Kitten survival rates are for male and female kittens combined.<sup>d</sup> The higher adult female survival is for females 37 to 60 months (4–6 years) old, and the lower survival is for females 61 to 108 months (6 plus years) old.<sup>e</sup> Survival rates of adults only. The variation is standard error.

Prior to wolf restoration in our study area, the median birth interval was 14.3 months (average = 16.0  $\pm$  5.9) for nine female cougars. Female cougars we monitored during wolf restoration had a somewhat longer median birth interval of 19.1 months (average = 19.3  $\pm$  7.5) [6]. These birth intervals generally aligned with the range of 17 to 24 months reported in other study areas (Logan et al. 1986; Ross and Jalkotzy 1992; Logan and Sweanor 2001; Robinson and DeSimone 2011). When we standardized our comparison by considering only birth intervals where at least one kitten in the litter survived to dispersal, the birth interval was a median of 10 months longer in the DW study (22.0 months versus to 12.2 months) compared to the PW study and averaged 5 months longer in the wolf restoration study (average of 21.5  $\pm$  7.5 months compared to 12.7  $\pm$  2.1 months) [7].

## DID WOLF PRESENCE ALTER MATERNITY RATES?

We calculated maternity rate ( $m_x$ ) as the average number of kittens born per reproductive female per year across all years (Caswell 2001). This amounted to a total of 43 female years prior to wolf restoration and 61 female years during wolf restoration. The PW maternity rate of 1.65 was higher than the DW maternity rate, which was 1.08 [8]. When split by gender of kittens, adult female cougars had average PW maternity rates of 0.75 female kittens (95 percent confidence interval = 0.48–1.02) and 0.70 male kittens (95 percent confidence interval = 0.42–0.98). On average, these rates were higher than those of DW females: 0.44 female kittens (9 percent confidence interval = 0.24–0.63) and 0.54 male kittens (95 percent confidence interval = 0.31–0.78) per female per year.

**TABLE 15.2.** Proportion of radio-marked females producing new litters and supporting dependent offspring (14 to 18 months old) each year, 1988–92 and 1999–2004, on the Greater Yellowstone Northern Range, Montana and Wyoming.

| Year | With Kittens | No. New Kittens | Total Females | With Dependent Young | Solitary Females | Proportion with New Litters | Proportion with Dependent Young |
|------|--------------|-----------------|---------------|----------------------|------------------|-----------------------------|---------------------------------|
| 1988 | 2            | 3               | 5             | 3                    | 2                | 0.40                        | 0.40                            |
| 1989 | 6            | 2               | 8             | 5                    | 3                | 0.75                        | 0.75                            |
| 1990 | 7            | 1               | 8             | 7                    | 1                | 0.88                        | 0.88                            |
| 1991 | 8            | 0               | 8             | 8                    | 0                | 1.00                        | 1.00                            |
| 1992 | 4            | 6               | 10            | 5                    | 5                | 0.40                        | 0.40                            |
|      |              |                 |               |                      | Mean             | 0.69                        | 0.72                            |
|      |              |                 |               |                      | SD               | 0.27                        | 0.21                            |
| 1999 | 2            | 2               | 4             | 4                    | 0                | 0.50                        | 1.00                            |
| 2000 | 5            | 2               | 7             | 6                    | 1                | 0.71                        | 0.86                            |
| 2001 | 2            | 9               | 11            | 9                    | 2                | 0.18                        | 0.82                            |
| 2002 | 6            | 7               | 13            | 7                    | 6                | 0.46                        | 0.54                            |
| 2003 | 7            | 7               | 14            | 9                    | 5                | 0.50                        | 0.64                            |
| 2004 | 2            | 8               | 10            | 7                    | 3                | 0.20                        | 0.70                            |
|      |              |                 |               |                      | Mean             | 0.43                        | 0.76                            |
|      |              |                 |               |                      | SD               | 0.20                        | 0.17                            |

Although maternity rates echoed the sex ratio bias toward males in the DW study as compared to the PW study, the maternity rate of male offspring was not substantially different between the study phases [9].

Maternity rates are a function of four elements: (1) litter size, (2) the age at which females first breed, (3) the proportion of females breeding, and (4) the interval between successive births. Because litter sizes were essentially equal prior to wolf restoration and when wolves were present—contrasting with our predictions—what might explain the longer birth interval and lower maternity rates we observed as wolves recolonized the study area? Although the age at which females first breed is influenced by philopatric females producing more quickly (Logan and Sweanor 2001), overall the younger age structure of PW females as compared to older DW females did not influence the number of kittens females produced. Female cougars greater than six years old produced litters at a frequency no different than that of two- to six-year-old females (Biek et al. 2006d) [10]. Logan and Sweanor (2001) also reported that reproductive activ-

ity remained high as female cougars aged, emphasizing that females producing the most litters and those that generally have the greatest reproductive success are those that live the longest lives. These two reproductive traits—litter size and lack of variation in reproductive activity by age—are under relatively strong selection pressure and tend to be traits with less intraspecific variation than survival rates (Charnov 2001; Cougar Management Guidelines Working Group 2005).

If kitten survival was lower during than prior to wolf presence, then females should produce litters again more quickly, and we would expect maternity rates to increase. In contrast, the survival of kittens increased during wolf presence compared to the PW period. We suspected that kittens survived longer because they benefited from their mothers' protection for longer periods than did PW offspring, which we delve into further in chapter 16. Prior to wolf restoration, an average of 69 percent of radio-marked resident females produced new litters each year. During wolf restoration, a lower proportion of radio-marked females—43 percent—producing litters each year was linked to females supporting their offspring for longer periods and hence a longer interval between successive births. In combination, these findings indicated that maternity rates were probably most strongly influenced by the time between subsequent births and thus the proportion of females producing new litters each year.

An abundance of vulnerable prey may also have contributed to increased maternity rates of PW female cougars. But maternity rate was not obviously sensitive to the decline in prey following wolf restoration, as we would also expect a lower mean litter size in conjunction with a lower maternity rate. In their New Mexico study, Logan and Sweanor (2001) likewise found that maternity rates were not obviously sensitive to a decline in the deer population during a drought. However, maternity rates they report were lower in a reference area where cougars were not removed (maternity rates of 1.3 and 1.4 following and prior to the deer decline, respectively) compared to a treatment area where greater than 50 percent of cougars were translocated out of the area (maternity rates of 1.6 to 2.0 prior to and during the deer decline, respectively). Although they do not indicate whether birth intervals or timing of independence and dispersal of offspring differed between the treatment and reference areas, the treatment area should have enabled greater opportunity for female offspring to remain philopatric and mothers to produce again quickly.

In another study in Montana's Garnet Hills, mean maternity rate was somewhat lower during a period of heavy hunting (mean of 1.08) compared to a period when the population was protected (mean of 1.40), although the difference was not statistically significant (Robinson and DeSimone 2011). Because litter sizes and birth intervals were not affected by hunting, the moderate difference in maternity rate could have been related to greater loss of females and offspring during hunting.

Although more data are needed to examine influences on maternity rates, we hypothesize that they are most strongly constrained by the length of time a mother supports her offspring, which may be influenced by several factors, including the carrying capacity of the environment for cougars and the risks associated with a greater density of dominant competitors. In chapter 16 we consider two indirect explanations for increased support of offspring prior to dispersal—and hence lower maternity rates—that seem plausible, although non-exclusive of each other: (1) density dependence and habitat quality and (2) experience and protection provided to young.

### REPRODUCTIVE SUCCESS OF MALES

Of eleven PW and eight DW radio-marked adult males, we documented five and nine breeding associations, respectively, using telemetry, yet 30 and 31 litters, respectively, were produced during the studies. Although we monitored radio signals almost daily and obtained locations weekly, it was easy to miss associations. Following wolf restoration, we attempted to use DNA to link fathers to offspring, but we were able to determine the sires for only 10 litters because of the loss of genetic samples from various storage facilities. In combination with litters produced following male-female associations determined by telemetry, we found that six males sired 15 litters, with four of them fathering 80 percent of the litters. Although our genetic data were limited, Murphy (1998) found that estimates of paternity obtained using telemetry yielded the same results as those based on microsatellite DNA analysis. His analyses revealed that nine males sired 23 litters for which paternities were estimated, with four of eleven radio-marked males fathering 78 percent of the litters. These findings suggested that fathers can be estimated reliably using field methods, but frequent monitoring is necessary. Estimates based on DNA remain preferable because, as we have described, females can consort with more than one male over long periods of time, confusing us as to which male sired the resulting litter.

Although male survival declined slightly following the restoration of wolves, male success at siring offspring apparently did not change. Resident males sired similar numbers of litters prior to and during wolf restoration. Similar to female cougars and to males of other large cat species, male cougars with the greatest longevity and those holding territories for longer periods had the greatest reproductive success and hence fitness (Packer et al. 1988; Smith and McDougal 1991; Murphy 1998; Logan and Sweanor 2001).

In polygynous breeding systems, direct competition between males for access to mates may be intense. Murphy (1998) found that although tenured males were occasionally challenged, their ability to defend their territories against intruders was an important link to their reproductive success. Prior to wolves, male reproductive success was correlated with male age, while the size of a male's territory had little influence on his reproductive success (Murphy 1998). In both our study periods, territorial males killed yearling males that lingered within the dominant male's territory. Younger males that announced their presence may have been particularly vulnerable to interactions that resulted in their death, as our observations indicated. At some point, however, age may work against males. As males near senescence, their physical ability to defend a territory successfully against young immigrating challengers apparently declines (Logan and Sweanor 2001).

Apparently more important than territory size is the number of females with which a male overlaps, as males with large territories sired few litters unless their ranges encompassed three or more females. The fidelity of males to their territories and their overlap with females increased following wolf restoration, which may have enhanced males' relationships with resident females and their ability to locate females in estrus, but did not alter the number of litters resident males fathered during the two study periods. Although males in hunted populations may sire litters at as young as fifteen months of age, male tenure has important implications for individual reproductive success as well as for delivering to offspring beneficial traits that may be lost when many males are removed through heavy harvest (Murphy 1998).

### CAUSES OF DEATH AND SURVIVAL RATES OF COUGARS

Because survival is best evaluated by following the fate of individuals over time, radio-collaring virtually all individ-



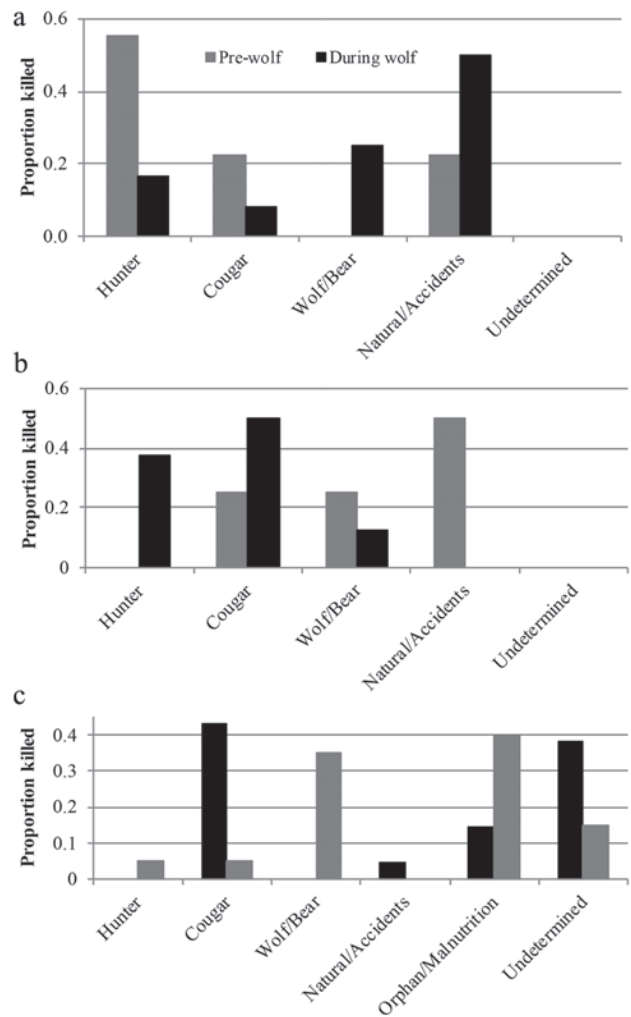
uals in the study area allowed us to monitor their survival and determine causes of mortality in most instances. We described our methods in greater detail in chapter 3. These cause-specific mortality and survival data, collected over fourteen years, allowed us to assess whether wolf restoration and other factors affected cougar survival. Our analyses further enabled us to reference cougar survival spatially to the landscape using models—which then resulted in maps showing areas of high and low risk of death for cougars (Ruth et al. 2011).

To make comparisons to data collected prior to wolves, we restricted data to a spatial subset of the study area where we had equal monitoring efforts during both study periods. We estimated survival of tagged and radio-collared individuals within that boundary only. Other radio-collared cougars died outside this boundary, but they were not included in the following summary for consistency of comparing survival and causes of mortality between the two study periods.

We estimated survival rates using known fates of cougars in Program MARK (White and Burnham 1999; Haroldson et al. 2006; Ruth et al. 2011). Equally important was understanding what factors most influenced cougar survival—was it their sex and age, wolf numbers, human harvest outside the park, the availability of elk, or other cougars, to name a few factors we considered. Hence we assessed various demographic, seasonal, and landscape variables that we hypothesized would explain variation in cougar survival. Following is a summary of the results of our survival analysis, presented in detail by Ruth and colleagues (2011), and further discussion of the implications of cougar survival during our study.

### INDEPENDENT COUGARS: CAUSES OF DEATH AND FACTORS INFLUENCING SURVIVAL

For adult and independent pre-dispersal cougars, we monitored 50 PW (30 females, 20 males) and 54 DW (27 females, 27 males), for a total of 1,911 cougar months (Ruth et al. 2011). We monitored a similar number of cougars each year during our PW and DW studies (Murphy 1998; Ruth et al. 2011) and kept tabs on female and male cougars for similar lengths of time in the two study phases (table 15.3). We confirmed 13 PW deaths (8 females, 5 males) and 19 DW deaths (11 females, 9 males) during our studies. We were able to assign a cause of death in all these cases.



**FIGURE 15.4.** Causes of death in cougar adults (a; PW n = 9; DW n = 13), independent subadults (b; PW n = 4; DW n = 7), and kittens (c; PW n = 21; DW n = 20) on the Greater Yellowstone Northern Range, 1987–94 and 1998–2005.

Cougars in the Northern Range were killed by other cougars (i.e., intraspecific aggression) and by wolves and bears (i.e., interspecific aggression). They also died while trying to kill prey, in falls from cliffs, from diseases, and from interactions with competitors, and some were killed by hunters north of the park boundary. These causes of mortality—human, predation, and natural-accidental—were similar between the PW and DW study phases (Ruth et al. 2011). Most deaths resulted from natural causes—62 percent prior to wolves and 75 percent during wolf restoration (fig. 15.4a, 15.4b). Before

**TABLE 15.3.** Numbers of adult and independent, non-dispersing cougars, total and average months radio-monitored, and mortalities by study phase and sex for cougars on the Greater Yellowstone Northern Range, 1987–2005 (adapted from Ruth et al. 2011).

| Study Phase | Sex      | No.<br>Cougars | Months Available |      |        |       | No.<br>Kittens | Months Available |     |        |       |
|-------------|----------|----------------|------------------|------|--------|-------|----------------|------------------|-----|--------|-------|
|             |          |                | Mean             | SD   | Median | Total |                | Mean             | SD  | Median | Total |
| Pre-wolf    | Female   | 30             | 19.3             | 20.4 | 10.0   | 578   | 27             | 5.7              | 4.3 | 5.0    | 155   |
|             | Male     | 20             | 14.3             | 17.3 | 7.5    | 285   | 27             | 6.1              | 4.0 | 5.0    | 165   |
|             | Subtotal | 50             | 17.3             | 19.2 | 9.0    | 863   | 54             | 5.9              | 4.1 | 5.0    | 320   |
| During wolf | Female   | 27             | 28.3             | 25.9 | 19.0   | 764   | 24             | 8.3              | 6.2 | 6.5    | 197   |
|             | Male     | 27             | 10.5             | 13.0 | 4.0    | 284   | 28             | 8.9              | 5.0 | 8.5    | 250   |
|             | Subtotal | 54             | 19.4             | 22.2 | 11.5   | 1,048 | 52             | 8.6              | 5.5 | 7.0    | 447   |
| Total       |          | 104            | 18.4             | 20.7 | 10.0   | 1,911 | 107            | 7.2              | 5.0 | 5.0    | 767   |

the arrival of wolves, most natural deaths were caused by disease or accidents ( $n = 4$ ) and intraspecific killing ( $n = 3$ ). One subadult female was killed by an unknown predator, a bear or coyotes, but she was also malnourished, which may have hampered her ability to escape the attack. The remainder of deaths, 38 percent ( $n = 5$ ), were a result of hunting north of the park boundary. During wolf restoration roughly one-third of cougar deaths resulted from each of three causes: intraspecific killing ( $n = 5$ ), killing by wolves ( $n = 4$ ), and disease or accidents ( $n = 6$ ). As in the PW period, the remainder of deaths—25 percent ( $n = 5$ )—were a result of human harvest.

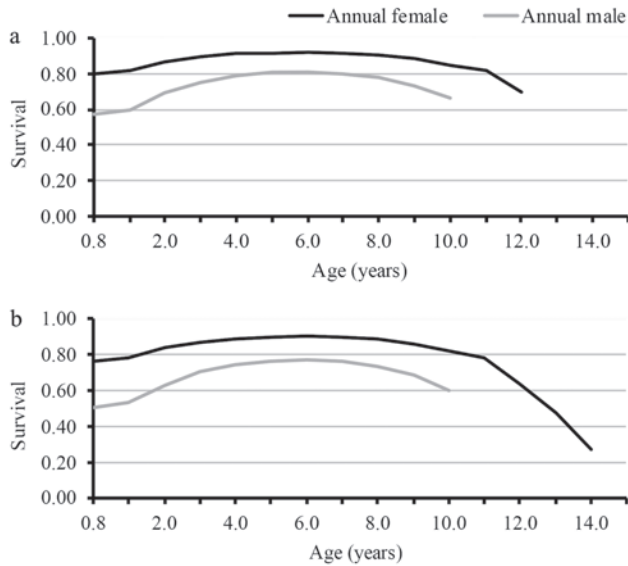
From year to year, survival rates of adult and independent subadult cougars did not vary substantially. Contrary to our predictions of substantially lower survival during wolf restoration, annual survival rates of independent female cougars were relatively high and were similar between the two study phases—0.88 (SE = 0.002) prior to wolves and 0.84 (SE = 0.008) during wolf restoration. Although younger males in the PW study had somewhat higher annual survival rates—averaging 0.75 (SE = 0.008)—than their DW counterparts, our survival analyses found the difference between the study phases was not substantial (Ruth et al. 2011). In contrast, survival of DW adult males was somewhat lower—averaging 0.68 (SE = 0.027). Males during wolf restoration did not survive as long, mostly because they were older when we first began monitoring them.

Gender and age of individuals had much larger influences on survival of cougars than did differences between study phases (Ruth et al. 2011: tables 2 and 3). Between one and ten years old, female cougars had high survival—greater than 0.80—but their survival rapidly declined beyond eleven years of age (fig. 15.5a, 15.5b). Average annual survival

for males varied between 0.70 and 0.81 between the ages of three and nine years. Males did not survive beyond eleven years in either study. When considered separately, subadult females within the study area had slightly lower survival rates than adults, whereas subadult and adult males had similar survival rates (fig. 15.6a, 15.6b).

Other factors that influenced survival were inter- and intraspecific carnivore density, the density of roads outside Yellowstone National Park, and elevation (Ruth et al. 2011: tables 2 and 3). As predicted, cougar survival did decline as wolf use increased, but the effect of increased wolf presence on cougar survival was small compared with effects of cougar age and gender, elevation, and density of roads where there was a hunting season. Although increasing wolf use did not play a strong role in explaining variation in cougar survival, cougars responded to increasing wolf use by concentrating their activities in more forested and topographically complex habitats, which did not always keep them safe. Contrary to our prediction that adult cougars would successfully evade capture by wolves because they readily climb trees, one adult male and two female cougars were killed by three different wolf packs in and near forested areas in winters 2002–3, 2003–4, and 2004–5. This amounted to 15 percent of all adult and independent subadult cougar deaths—all occurring in winter.

Along with competition with wolves, we also predicted that increasing density of cougars could increase intraspecific interactions and competition for food, thus negatively affecting survival, particularly of mothers and dependent kittens. Indeed, 35 percent of PW deaths and 15 percent of DW deaths resulted from cougars killing each other. Prior to wolf restoration, this aggression was focused on kittens

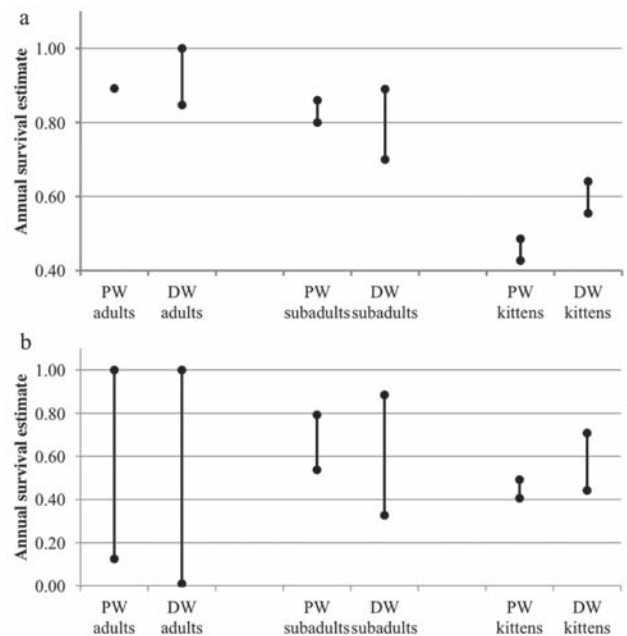


**FIGURE 15.5.** Annual, age-specific survival estimates of independent adult and subadult cougars within the study area prior to (A;  $n = 30$  female and 20 males) and during wolf restoration (B;  $n = 27$  female and 27 males) on the Greater Yellowstone Northern Range, 1987–2005. We computed estimates using  $\beta$ s from top survival models (see Ruth et al. 2011 for details). Adults and independent, pre-dispersal subadults were combined because differences in their survival were best captured by age.

and maternal females—two maternal females were killed by males. A young subadult male cougar was also killed by a resident adult male during the PW period. Following wolf restoration, the aggression was primarily between dominant and subadult males (fig. 15.4a, 15.4b). Four subadults were killed by resident adult males, although one older male was also killed. In contrast to the PW study period, only two kittens were killed by male cougars during wolf restoration.

Differences in aggression between study phases were apparently associated with very stable and longer-term social relationships of cougars during wolf restoration relative to the early years of the PW study, which we discuss in more detail later. We found some support of this, as our survival models indicated that cougars survived better as the density of adult male cougars increased—but again, the effect was small compared to the larger influences of cougar age and gender, elevation, and density of roads where there was a hunting season (Ruth et al. 2011).

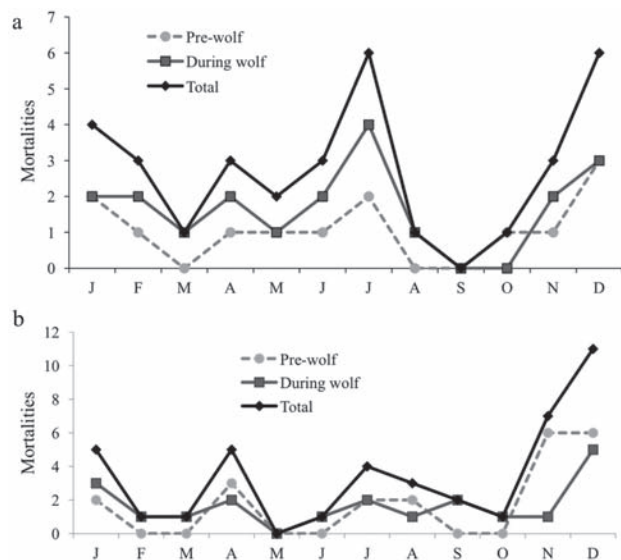
When we combined mortalities across years of each study phase, there was a similar pattern of mortalities for months



**FIGURE 15.6.** Annual survival of adult, subadult, and kitten female (a) and male (b) cougars prior to (PW) and during (DW) wolf restoration on the Greater Yellowstone Northern Range, 1987–2005.

of the year (fig. 15.7a). Cougar deaths peaked in December through January and again in July. While deaths in July were a mix of intra- and interspecific killing, accidents, and other natural causes, most cougars that died in the December and January peak were killed by hunters or wolves. As earlier noted, hunting along the northern boundary of Yellowstone National Park accounted for 38 percent and 25 percent of total mortality during the PW and DW studies, respectively. Deaths caused by hunters in our two study periods were distributed differently between adults and subadults. Hunters killed five radio-collared adult cougars during the PW study—three adult males, one solitary adult female, and one maternal female, F15. After her death, all three of F15's five-month-old kittens did not survive. During wolf restoration, two radio-collared adult females and three radio-collared subadult males were killed by hunters. Adult males during the study resided primarily in the park until after our study ended. Cougars were also killed by wolves during winter, but not all deaths were limited to December and January.

Adult and subadult cougars in our study sample spent proportionally more time in areas with no hunting access (national park or wilderness areas)—they spent only about



**FIGURE 15.7.** Total monthly mortalities of adult and independent subadult male and female cougars (a) documented prior to ( $n = 13$ , 1987–95) and during wolf ( $n = 20$ , 1998–2005) restoration on the Greater Yellowstone Northern Range study area. Total monthly mortalities of male and female kittens (b) documented during the PW ( $n = 21$ , 1987–95) and DW ( $n = 20$ , 1998–2005) study phases.

27 percent of their time in areas open in winter to hunting. Yet road access had a significant negative effect on survival for cougars that overlapped or lived outside the park during winter (Ruth et al. 2011). Survival of Northern Range female cougars dropped below 0.80 at road densities exceeding 0.75 km/km<sup>2</sup>, and male survival rapidly fell below 0.80 at road densities exceeding 0.35 km/km<sup>2</sup>, perhaps indicating selection for male cougars by hunters (Ruth et al. 2011). Road densities above 1.58 km/km<sup>2</sup> had no additional effect on survival, as estimated survival of females and males dropped to zero. Because we excluded them from analysis once they dispersed beyond the study boundary, our study sample underrepresented the effects of hunting on subadults. Of thirty-eight successful dispersers in our during wolf restoration study, 29 percent were killed during the hunting season at eighteen months to three years of age, and 18 percent were killed during the hunting season at greater than three years of age.

Although we linked survival to interspecific, intraspecific, and hunting-caused mortality, we could not explain all proximate causes of mortality with factors used in our survival analysis for adults, independent subadults, or kittens. This included 30 percent of the adult and independent subadult

cougars we monitored and at least 30 percent of the kittens we monitored in the two study periods that died from accidents, disease, and other unknown natural deaths (fig. 15.4). For instance, prior to wolves, adult female F11 died from a vaginal infection. During wolf restoration, both five-year-old male M139 and nine year-old F111 died in falls from cliffs. Both male M139 and the bighorn ram he was attempting to kill died in a 122-meter fall off the cliffs of Mount Norris in November 2001 (see full report in Ruth 2004b and Murphy and Ruth 2010). Dependent kitten M145 was orphaned by his mother, F105, around April 27, 2001, when he was 10.8 months old, while she kept his two siblings. He was abandoned at an elk calf kill, wandered around alone for seven weeks, and was bitten by a rattlesnake during that time. Although M145 probably would have died from his poor condition—he weighed only 16 kilograms (35 pounds) and was malnourished (table 15.4)—the snake bite was the proximate cause of death.

## KITTENS: CAUSES OF DEATH AND FACTORS AFFECTING SURVIVAL

Prior to wolf restoration, 27 male and 27 female kittens were radio-tracked within the survival study area (Murphy 1998). We radio-tracked another 28 male and 24 female kittens during wolf restoration. We radio-collared between 57 percent and 78 percent of PW kittens and 60 percent to 70 percent of DW kittens prior to 3.5 to 4.8 months of age (fig. 14.4a, 14.4b; Ruth et al. 2011). No kittens less than four weeks of age were radio-collared. In each study there were kittens in litters we were not successful at capturing for marking and others that were killed in the den prior to an age when we could mark them. Hence we based survival rates on those kittens we marked and followed. A cause of death was determined for 8 male and 5 female kittens during the PW study and for 10 male and 7 female kittens in the DW study (Ruth et al. 2011). Another 8 PW and 3 DW kittens died from undetermined causes.

Radio-marked kittens died from predation, orphaning or malnutrition, and unknown causes; within these broad categories, causes of death were similar in the PW and DW study phases (Ruth et al. 2011). Twenty-nine percent and 39 percent of total mortalities were a result of these natural causes prior to and during wolf restoration, respectively, but the distribution of deaths into finer categories was different [11]. Before the arrival of wolves, kittens died mostly from infanticide by adult male cougars—43 percent of all



**TABLE 15.4.** Weights and femur marrow fat values (FMF) of fourteen cougars at mortality on the Greater Yellowstone Northern Range, 1998–2005.

| Date of Death | Cougar ID | Age (yrs) | Weight (kg) | FMF (%) | Cause of Death            |
|---------------|-----------|-----------|-------------|---------|---------------------------|
| 16 Dec 1999   | F108      | 0.4       | 7.6         | —       | Wolves                    |
| 16 Dec 1999   | M138      | 0.4       | 7.6         | —       | Wolves                    |
| 15 Jun 2001   | M145      | 0.9       | 16.0        | 53.2    | Starvation and snake bite |
| 15 Jul 2001   | M144      | 3.0       | —           | 85.2    | Cougar                    |
| 27 Nov 2001   | M139      | 6.3       | 57.5        | 84.8    | Fall from cliff           |
| 8 Dec 2001    | F105      | 7.4       | —           | 87.0    | Hunter                    |
| 9 Aug 2002    | F017      | 14.0      | —           | 90.0    | Unknown natural           |
| 11 Oct 2002   | M151      | 0.3       | 7.5         | 90.7    | Cougar                    |
| 19 Dec 2002   | M141      | 2.5       | 63.6        | 81.5    | Hunter                    |
| 3 Apr 2003    | F106      | 9.7       | 55.0        | 91.6    | Wolves                    |
| 10 July 2003  | F111      | 9.0       | —           | 76.3    | Fall from cliff           |
| 2 Feb 2004    | F053      | 14.5      | —           | 93.1    | Wolves                    |
| 22 Jun 2004   | F102      | 5.9       | 40.0        | 78.2    | Unknown natural           |
| 21 Nov 2004   | M127      | 6.4       | —           | 75.4    | Wolves                    |

kitten mortalities—and we suspected that two of the undetermined deaths were also a result of infanticide (fig. 15.4c). During wolf restoration there was greater territorial stability of dominant adult males, and we documented only one (5%) kitten mortality caused by infanticide (fig. 15.8). Instead, 35 percent of mortalities during wolf restoration resulted from predation by wolves and bears. We speculated that the greater number of kittens that died from orphaning and malnutrition during wolf restoration—40 percent as compared to 10 percent prior to wolves—was related to increased competition for resources. Yet timing of birth may also have played a role. For instance, female F107 lost all three of her litter, which was born later than most on October 22, 2003, as she moved the kittens from her summer to winter range through deep snows. All three kittens died of starvation at three months old between January 28 and 31, 2004.

Contrary to our predictions, dependent kittens had a higher annual survival rate of 0.585 (standard error = 0.02) during wolf presence than prior to wolf presence—about 0.46 (SE = 0.004) in the PW study. Unlike among adult cougars, the gender of kittens had little influence on their survival to independence from their mother, which was similar to kitten survival in New Mexico and Idaho (Logan and Sweanor 2001; Laundré et al. 2007). The annual survival rate of PW

**FIGURE 15.8.** Before the arrival of wolves on the Greater Yellowstone Northern Range, 43 percent of all kitten deaths resulted from infanticide by adult male cougars. Relative to the PW period, there was greater territorial stability of dominant adult males during wolf restoration, and we documented only one kitten death as a result of infanticide. Instead, 35 percent of kitten deaths were caused by wolves and bears.

male kittens was 0.45 (SE = 0.02), and PW female kittens had a similar rate of survival at 0.48 (SE = 0.005) (fig. 15.6a, 15.6b). During wolf presence, annual survival of male and female kittens was 0.58 (SE = 0.07) and 0.60 (SE = 0.02), respectively.

Kittens of both sexes in our studies had higher mortality between five weeks and four months of age, similar to findings of Logan and Sweanor (2001). As kittens grew beyond four months, their likelihood of survival increased rapidly and reached an asymptote of 0.90 between seven and eight months (0.6 to 0.7 years) of age (Ruth et al. 2011: fig. 2A). Although wolf presence had a mostly negative effect on kitten survival, as in adult cougars the effect was small compared to other factors that clearly influenced kitten survival—such as kitten age, season, and biomass of elk calves (Ruth et al. 2011: tables 5 and 6).

Older cougar mothers, with their increased experience in raising offspring, could have a positive influence on survival of dependent young, as reported for African wild dogs and grizzly bears (Creel and Creel 2002; Schwartz et al. 2006c). In our competitor-rich system, we predicted that older, more experienced females should have greater success at keeping their young safe, yet we did not find a clear relationship that kittens born to older mothers had improved survival [12]. Several factors may influence the relationship between age

of the mother and survival of her offspring. First, there appeared to be high variation in kitten survival across female ages. Several highly productive prime-age females experienced low success in rearing offspring to independence, while others consistently raised young to independence and dispersal. In both the PW and DW studies, survival of breeding age females was high, and we documented one kitten of the year with an adult female known to be eleven years old. Second, philopatric females have first litters at a younger age, and these litters may have higher survival than those of non-philopatric females (Murphy 1998; Logan and Sweeney 2001: 117). As a result, offspring born to young mothers are likely to have survival rates similar to the offspring of older mothers if they are philopatric on the study area. Because experienced females produced litters intermittently, environmental and other factors, rather than breeding experience, influenced the frequency at which they produced litters (Murphy 1998) as well as the survival of those litters to independence.

In addition to improved survival as they grew older, the survival of kittens improved with increased availability (i.e., biomass) of elk calves. Their survival also improved during summer and as the density of adult males (our index of male territorial stability) increased (Ruth et al. 2011). In northern climates mothers may have greater difficulty feeding and protecting mobile kittens as the family group moves through deep snows following prey from summer to winter range. In both study periods kitten deaths peaked in November through January and again in April; thus kitten survival of 0.76 during winter was lower than mean kitten survival of 0.91 during snow-free months (fig. 15.7b; Ruth et al. 2011: fig. 2b). Most kitten mortality we documented in winter was associated with infanticide in the PW study, while wolves, orphaning, and malnutrition dominated in the DW period [13].

We expected similar rates of infanticide during wolf restoration to those before wolf presence if predation or competition for food resources were strong motives for infanticide (Ruth et al. 2011). Thus, on the one hand, we predicted that increased density of adult males should increase the odds that kittens were encountered and killed and would negatively influence the survival rate of kittens. On the other hand, stability of territorial males that dissuade activity of other males should reduce infanticide and have a positive influence on kitten survival (Logan and Sweeney 2001, 2010). In our survival models, the increasing density of adult males during winter (as our index of male territory stability) did

have a positive influence on kitten survival, but the overall effect was small compared to other factors that clearly influenced kitten survival—such as kitten age, season, and biomass of elk calves (Ruth et al. 2011).

Overlap between male and female cougars increased on winter range and coincided with breeding, which began in January–February and peaked in March–April during both study phases. Such increased overlap apparently increased chances that adult males encountered females unfamiliar to them or unattended litters, with infanticide a result of males probably seeking breeding opportunities prior to wolf presence (see also Logan and Sweeney 2001). Yet in five cases of infanticide in the PW study, it was unclear whether infanticidal males were sires of litters they killed or the sires of subsequent litters. Although cougars were even more condensed on winter range as they avoided wolves, infanticide occurred only once. In this case the kitten's death was coincident with the arrival of a new male that established in male M149's home range after he died. Evidence of the stabilizing effect of territorial males and reduced infanticide and, conversely, high turnover of males and increased infanticide has been found in a variety of mammals as diverse as grizzly bears, African felids, and baboons, and there is increasing evidence from cougars (Whitman et al. 2004; Bellemain et al. 2006; Cooley et al. 2009; Balme et al. 2010; Moscovice et al. 2010).

Considering the number of encounters with dominant competitors we documented at kill sites, cougars were generally quite successful at avoiding injury or death. Adult cougars were generally proficient at seeking rock outcrops and climbing trees to escape pursuit by wolves or bears (Ruth 2004a). Yet wolves killed five kittens and three adult cougars, orphaning another two kittens that eventually died of starvation. Kittens, especially young of the year, typically lack the experience and knowledge of their home range to seek out appropriate escape cover—instead hunkering down in cover on the ground or climbing trees that lack ample branches for perching for long periods of time. Female F107 lost her entire litter of four kittens to the Druid Peak pack as the family group scattered after they were chased from their kill. When following their mother through deep snow, kittens easily travel in her tracks, but when chased, these five-month-old kittens were not successful at plowing through the loose, deep powder to evade wolves. In another instance, two five-month-old male kittens were orphaned after their mother, F106, was killed by the Leopold pack on Mount



**FIGURE 15.9.** Yellowstone National Park biologist Dan Stahler examines maternal female cougar F106 within hours of her fatal encounter with the Leopold pack. Her two orphaned five-month-old kittens later died of malnutrition. Photo by Mike Sawaya, Hornocker Wildlife Institute/Wildlife Conservation Society.

Everts (fig. 15.9). They stayed near where she had left them and eventually succumbed to starvation. In total, these kitten deaths caused by wolves represented 10 percent to 39 percent of observed average annual kitten production (10.2 kittens/yr over 6 years) on the Northern Range. In terms of whole litters, the deaths represented 7 percent to 23 percent of observed average annual litters produced (4.3 litters/yr over 6 years; Ruth et al. 2011). All but one of these deaths occurred during winter. While occasional loss of kittens should generally cause little or no change in population dynamics, the loss of prime-age females is expected to have a stronger effect on population dynamics (Creel et al. 2001).

## **PATHOGENS**

Although they often receive less attention than hunting, accidents, and intraspecific killing as causes of death, infectious diseases can strongly influence natural populations, and their effects are often difficult to document (Roelke-Parker et al. 1996; Creel and Creel 2002). With increased human development and recreation in remote areas, wildlife exposure to diseases that commonly affect domestic animals has increased in national parks and other remote areas (Aguirre et al. 1995; Gillin et al. 2002).

During our study we collaborated with researchers at the University of Montana to understand better the role of pathogens in Yellowstone and in three other populations in Wyoming and Montana (Biek et al. 2006c, 2006d). This

serological survey found that cougars in Yellowstone and the other populations had been exposed to plague, canine distemper, feline immunodeficiency virus (FIV), feline parvovirus, feline coronavirus, and feline calicivirus (Biek et al. 2006c). Feline herpesvirus was absent in all four populations.

Prevalence of the bacterium *Yersinia pestis* in our study, in Montana, and in Wyoming was less than 28 percent, sporadic, and noticeable only for short periods of time (Biek et al. 2006c). Increased incidence in certain years likely reflected higher transmission from an unknown reservoir host species, resulting in simultaneous exposure of multiple cougars. These temporal fluctuations fit observations based on serological data in Yellowstone coyotes, for which prevalence fell from 57 percent in 1991 to zero in 1993 (Gese et al. 1997). Prior to arrival of wolves, no cougars were known to have died from plague. Rapid autolysis of tissue can limit effective isolation of the pathogen in the lab, and it may at times go undetected (Logan and Sweanor 2001). Yet serological data indicated that exposure to the bacteria was more consistent in Yellowstone cougars during the years 1998 to 2003 than during the pre-wolf period (Biek et al. 2006c: 611, fig. 3c). After wolf restoration we documented flea infestation on three female and two male cougars during winter captures. Two female cougars died from plague, one in June 2004 and the other in June 2005. Female F47 was known to be seropositive prior to her death in 2005. Only female cougars exhibited an increased probability of exposure to plague as they aged—35 percent were plague positive as adults (Biek et al. 2006c).

In addition to plague, Greater Yellowstone Northern Range cougars also appeared to experience isolated outbreaks of canine distemper virus (CDV) in 1991 and 1999, although overall antibody prevalence was less than 15 percent (Biek et al. 2006c). The outbreaks were not directly linked to domestic dogs, but they appeared linked to discrete, multi-host outbreaks of CDV, as Yellowstone coyotes experienced CDV outbreaks in 1991, 1999, and 2005. Yellowstone wolves also experienced CDV outbreaks in 1999, 2002, and 2005 (Gese et al. 1997; Almberg et al. 2009). Although years of high wolf pup mortality in 1999 and 2005 in the northern region of the park were correlated with peaks in CDV seroprevalence, we found no evidence that CDV substantially influenced cougar survival.

Cougars are natural hosts for FIV, and up to 60 percent of individuals in a cougar population can be infected with



FIV<sub>Pco</sub> (Olmsted et al. 1992; Carpenter et al. 1996; Biek et al. 2003). In Yellowstone there were noticeable differences between males and females in exposure to FIV (Biek et al. 2006a, 2006b, 2006d). The probability of exposure increased rapidly with male age but much less so with female age. Overall, a low proportion of Yellowstone females had FIV, but all kittens that were infected with FIV were offspring of infected mothers (Biek et al. 2003; Biek et al. 2006c). In Yellowstone and in the Snowy Range of Wyoming, FIV-infected female cougars had a tendency toward lower reproductive performance—supporting a hypothesized increased abortion and kitten mortality among FIV-infected females, as seen in domestic cats (Biek et al. 2006d). Given conditions in the Yellowstone population through 2005, we did not expect any reduction in fecundity as a result of FIV strongly affecting cougar population growth. In addition, although cougars studied in Montana and Wyoming were infected with FIV, the infection did not appear to predispose them to a higher probability of becoming infected with the other common feline microparasites (Biek et al. 2006d). The lack of pathogenic effects on wild felids is viewed as supporting a theory of coadaptation among FIV-like viruses and their wild feline hosts (Carpenter and O'Brien 1995).

Feline parvovirus (FPV) is endemic in cougars, and Yellowstone cougars showed high—58 percent—antibody prevalence for the virus (Biek et al. 2006c). As with FIV, exposure to FPV and to CDV increased as cougars aged. This might be because age increases the probability of experiencing a local outbreak of an epidemic pathogen, or it might correlate with cougars entering a new life stage in which physiologic or behavioral changes resulted in higher exposure risk. Feline parvovirus has occasionally been associated with considerable mortality (Wassmer et al. 1988), but detecting the virus postmortem as well as teasing out its contribution to a death is difficult, hence our uncertainty as to how FPV affected cougars in our study.

## SURVIVAL IN COMPARISON TO OTHER STUDY POPULATIONS

Table 15.1 summarizes data on annual survival for seven hunted and non-hunted cougar study populations. Survival rates of adult and subadult Northern Range cougars were similar to mean annual survival estimates from lightly hunted to non-hunted study populations (Logan and Sweanor 2001). As in other studies of hunted cougar populations and

in contrast to one non-hunted population in New Mexico, female cougars in our study area had higher survival than males. Only Logan and Sweanor (2001) have found higher natural survival for male cougars, with one male living to slightly over twelve years old. Because all the studied areas (except for cougars in Logan and Sweanor's study) experienced some human hunting, selective harvest of males could have contributed to observed differences in female and male survival in our study.

Prior to wolf restoration, 73 percent of harvest on the north end of our study area, outside Yellowstone Park, was males, suggesting selection for this gender. During wolf restoration, males (55%) and females (45%) were harvested more equitably (Ruth et al. 2011). The harvest structure of adults and subadults differed during our two studies—hunters removed only subadult males in the DW study. Across all years of our study, annual hunter harvest of cougars along Yellowstone's northern boundary averaged 1.4 (range 0–2) adult females and 0.6 (range 0–1) one- to two-year-old females per year between 1988 and 2005. During the same time span, annual hunter harvest averaged 1.8 (range 0–3) adult males and 0.9 (range 0–1) males that were one to two years old. These removals reveal few biases toward males. The mean rate of harvest of 0.4 to 0.8 cougars per 1,000 km<sup>2</sup> (95 percent confidence interval) was relatively low compared to other hunted areas in Montana (Newby et al. 2013). For instance, 1.5 to 7.2 cougars per 1,000 km<sup>2</sup> (95 percent confidence interval) were killed in hunt districts adjacent to a study area in the Garnet Range in western Montana (Robinson and DeSimone 2011). Hence, although our study area was not isolated from the effects of hunting, even with high densities of competitors, cougar survival was relatively high and was most similar to lightly hunted or non-hunted study populations (see Logan and Sweanor 2001; Lambert et al. 2006; Quigley and Hornocker 2010).

In two landscapes dominated by wolves, survival rates of cougars were much lower than those for cougars during our study. Survival rates reported for cougars approximately ten years after wolf restoration in the North Fork of the Flathead River, Montana, were 0.29 for males and 0.65 for females (Ruth 2004a). In this system, hunting and starvation were principal sources of cougar mortality. Cougars lost their kills to bears during summer and to wolves and bears during winter, which, along with declining elk and deer numbers, probably played a role in their poor condition (Ruth 2004a).



During wolf restoration in Banff National Park, where hunting did not occur, Kortello and colleagues (2007) documented interspecific killing and poor condition of cougars, with annual survival of 0.51 for males and females combined. Both the North Fork of the Flathead and the Banff studies indicate that cougars are adept at avoiding direct mortality from competitors, but competition for limited prey can eventually lead to poor condition and starvation. Cougar survival remained high during our post-wolf restoration study period, perhaps because prey was not yet a limited resource and cougars were superior at exploiting rocky, forested landscapes that provided security from wolves and bears.

Kittens typically have lower survival rates—an average of 50 percent make it to dispersal age and 50 percent do not—than those of any other age class, with the exception of subadults that have left their home area (Quigley and Hornocker 2010). Kitten survival prior to wolves was considerably lower than in most hunted and non-hunted populations. During wolf restoration, kittens survived at a rate similar to those in the non-hunted New Mexico study and also similar to those in a heavily hunted population in Washington (Lambert et al. 2006). These discrepancies probably result from three factors. First, the way estimates were derived differed across studies, in part because of advances in analytical methods. Although kittens were marked at dens in our studies and theirs, when we used methods of Logan and Sweanor (2001), our cumulative kitten survival increased to 0.61 (21 of 54 died) prior to wolves and 0.62 (20 of 52 died) during wolf restoration, which mirrored their estimates. Second, including litters detected at ages older than three to four months, as was the case in the Washington study of Lambert and colleagues (2006), would result in estimates of survival that are biased higher than if kittens were detected prior to age three to four months. Lastly, whereas other studies reported loss of entire litters as the result of a single cause, independence of survival within litters was assumed in survival estimates, unlike our analyses; therefore these estimates of survival are not directly comparable to ours (see Ruth et al. 2011).

On the Greater Yellowstone Northern Range, kitten survival improved when elk calves were more available and declined when calves were less available. In contrast, Logan and Sweanor (2001) found that kitten survival did not appear to be sensitive to the population dynamics of deer, and they suggested that a time lag preceded lower survival in response to a reduced prey base, which was later

confirmed by Laundré and colleagues (2007). They found that survival of cougar young declined the year of and two years after a mule deer decline, but survival rates returned to pre-decline levels once cougar numbers adjusted downward to the lower abundance of prey. We found no support for effects of winter severity or summer precipitation on cougar survival on the Northern Range, but nutritional limitations that occur on summer range may predispose elk to nutritional effects that do not manifest until winter. In addition, there might be cumulative effects for elk that survive harsh winters in combination with limited nutrition on summer range over the long term (J. G. Cook et al. 2004). Future analyses could incorporate such lag and cumulative effects to evaluate the influence of climatic factors over the long term and improve our understanding of production of kittens and their survival.

Hunting shapes cougar survival in hunted populations and has the potential to reduce population levels quickly (Robinson and DeSimone 2011), which may also undermine adaptive social behavior that enables cougars to coexist in systems with wolves and bears. Several studies have now revealed that in heavily hunted areas, where high turnover of males results, kitten survival is reduced as a result of increased infanticide, of starvation after the mother was killed and kittens became orphaned, or perhaps as a result of both infanticide and starvation (Cooley et al. 2009; Robinson and DeSimone 2011). In the Garnet Hills, Montana, kitten survival soared to levels similar to those of adults once the study area was protected from heavy hunting (Robinson and DeSimone 2011). In the restoring Yellowstone cougar population prior to the return of wolves, kitten survival and infanticide initially mirrored the conditions of high male turnover and infanticide in hunted populations. Infanticide was concurrent with newly established males vying for territories (immigration rate of 1.7 per year), and some resident males killed kittens—perhaps because they were uncertain if they had fathered a litter—which negatively influenced kitten survival rates. Eventually, when cougars established well-defined territories and maintained them for longer periods, along with new males immigrating at about half the earlier rate (0.9 per year), kitten survival improved—even after the return of wolves. Hence as wolves were restored within the study area, we observed lower rates of infanticide, which we suspect were linked to greater territorial stability of adult males and females. In fact, the improved survival

of kittens probably resulted from mothers supporting and providing safety to their offspring for longer periods of time. Thus naturally low turnover and stable social relationships help cougars defend and provision offspring and benefit the mother through increased vigilance by growing young, all of which may be adaptive strategies for surviving in competitive environments.

In areas where cougars are hunted, the competitive equation may be altered, as wolves and black bears are also typically hunted annually. However, in the North Fork of the Flathead, Montana, the second main cause of mortality after hunting was starvation, suggesting that competition may not be moderated by hunting when prey are a limited resource important to carnivores and hunters alike (Ruth 2004a).

## SUMMARY

We documented reproduction and survival of cougars over a total of fourteen years—seven years prior to wolf restoration and seven years after wolves were restored. Competition with wolves did not alter the timing of breeding or birth or the size of litters, as compared to findings for cougars living in a wolf-free landscape. Litter sizes averaged 2.9 kittens in each study period and appear consistent with other studies across geographic ranges, moderate changes in prey abundance, densities of interspecific competitors, and hunted versus non-hunted populations. This information adds to growing understanding from long-term research that suggests little variation in litter size unless perhaps in extremes of limited food. The continued support of offspring as they grow is more closely tied to the abundance of vulnerable prey within a female's home range, the survival of mothers, and their ability to keep offspring out of harm's way. Although litter sizes were similar, maternity rates of female cougars were lower during than prior to wolf restoration. The number of DW females producing litters each year was linked to females supporting their offspring for longer and hence a longer interval between successive births than among PW females. Our findings indicated that maternity rates are probably most strongly influenced by the time between subsequent births and thus the proportion of females producing new litters each year, as there was lack of variation in litter size and in reproductive activity by age. A lower maternity rate might translate to fewer offspring emigrating to surrounding areas reliant on an influx of new individuals.

We followed the fates of 104 adult cougars and 107 kittens over fourteen years and determined their cause of death. This information also allowed us to assess survival rates and factors that explained variation in cougar survival prior to and during wolf presence. Before the arrival of wolves, natural deaths were predominantly from disease, accidents, and intraspecific killing; the remainder of adult cougar deaths—38 percent—resulted from human harvest north of the park boundary. During wolf restoration, natural adult cougar deaths resulted from intraspecific killing, deaths caused by wolves, and disease or accidents; the remainder of adult deaths—25 percent—resulted from human harvest north of the park boundary. The percentage of deaths that involved cougars killing each other was 35 percent prior to wolves and 15 percent during wolf restoration. Survival rates differed for kittens—the survival of kittens improved instead of declined following the return of wolves. Before the arrival of wolves, kittens died primarily from infanticide by adult male cougars—43 percent of all kitten mortalities; during wolf restoration there was greater territorial stability of dominant adult males, and we documented only one kitten mortality caused by infanticide. Instead, predation by wolves and bears caused 35 percent of mortalities during wolf restoration.

Adult and independent subadult males and females all had similar survival rates during wolf restoration, as did their PW counterparts. Road access had a significant negative effect on survival for cougars that overlapped or lived outside the park boundary during winter, and elevation also likely captured access to cougars by hunters starting from trailheads or roads originating in the Gardiner and Paradise Valleys. Cougar survival declined with increasing wolf use, and cougar survival increased with an increasing density of territorial adult male cougars—our index of increased social stability in our study population—but both had smaller influences on cougar survival than did effects of cougar age, gender, elevation, and density of roads where there was a hunting season for cougars. Improved survival of kittens during wolf restoration probably resulted from mothers supporting and providing safety to their offspring for longer periods of time. Stable social relationships and naturally low turnover boost survival through more extended maternal defense and provisioning of offspring and greater vigilance by the young, likely enhancing survival rates in competitive settings.

**Text Box 15.1. High- and Low-Profile Behaviors**

Between February 7 and March 14, 1999, eighteen-month-old male M126 hunted, rested, and made four kills during the thirty-six consecutive days we monitored him with radio-telemetry to determine his kill rate. He maintained a "low profile," as his movements covered an area of only 4.7 km<sup>2</sup>. When he made kills, he lingered at them longer than the average number of days it took most cats to feed on calf or adult elk kills. For instance, he spent seven days at his third kill of a calf elk, killed another calf elk the following day, and spent the next eight days at that kill site. It seems likely that he finished consuming each of these kills within three to four days but remained at them for several days longer. Between kills, he frequently spent time bedded in a cave-like compartment of a large pile of boulders. After failing in one attempt to kill an elk, he returned to the same "cave" and spent the following day there. Although he scraped on two occasions we discovered, he did so within the small area where he restricted his movements. Only once did he leave this area during the thirty-six-day period. While feeding on kill number four—a calf

elk—he made one excursion 2.4 km upriver, bedded, and was chased from his bed site by another male, presumably adult male M137. Upon returning to his small area he continued restricted, localized movements and apparently did not scrape through the end of our sampling effort. This low-profile strategy proved successful—male M126 eventually dispersed from the study area in the spring of 2000.

In contrast to this behavior, eighteen-month-old male cougar M129 traversed an area of roughly 35 km<sup>2</sup> as we followed him over twenty-six consecutive days to document his rate of killing prey. His movements overlapped those of resident adult males M137 and M148. Male M129 did not maintain a low profile but instead announced his presence through frequent scent-marking over this relatively large area. He associated with an unmarked female for at least two days near the beginning of the predation sequence. After the end of our kill rate sampling, male M129 moved downriver and was killed in a fight with another male, probably M137, on May 17, 1999.

**Text Box 15.2. Mating Behavior**

As we followed F106 each day from January 5 through March 13, 2001, to document her kill rate, we coincidentally documented her mating behavior during possibly a single estrous cycle but more likely multiple cycles. Over a period of sixty-eight days, she frequently made scrapes and urinated on them while spending a minimum of thirty days switching between mating with two different adult males. She first spent a minimum of twelve days with eight-year-old resident male M137. While they hung out together below the cliffs of Mount Everts, they yowled; on one day, from a distance, we observed F106 rolling in front of M137 while he rested in the shade near the cliff (fig. 15.1). They separated, and F106 killed a cow elk on January 21, which wolves quickly discovered. The wolves pursued F106 until she sought refuge in a tree, but they did not feed on the kill, and F106 eventually returned and fed through January 26. She then wandered alone beneath the cliffs of Mount Everts, where she left several scrapes, and traveled north to rocky outcrops along the south side of the Black Canyon of the Yellowstone River. From January 29 she again spent three days with M137 in the rocky, broken woodlands north of the river. They moved south of the river separately but were together again between February 4 and 9 as they traveled 8 km east upriver together, vocalizing frequently. After they parted ways this time, F106 quickly made a kill on February 11, where she remained for two days. On the fourth day after parting from her association with M137, she consorted with two-and-a-half-year-old philopatric male M127—offspring of female F123—for five days.

The day after she parted ways with M127, F106 traveled 19–20 km downriver and made her third kill—a cow elk—on February 18, where she fed alone over six days. Once she departed from this kill, she moved about for eight days and then killed and fed on a mule deer for four days, again adjacent to the cliffs of Mount Everts. She remained alone until March 10–12, when she spent two days with male M137, parted from him, and was with M127 the very next day, March 13, when our kill rate sampling sequence ended. Altogether, F106 covered an area of roughly 53 km<sup>2</sup>—including some areas outside her typical maternal range—as she spent at least twenty-four days with M137 and at a minimum six days with M127 during six separate associations. We suspected that M127 was the son of M137, but DNA collected from both males during capture revealed that they were not related. F106 produced a litter of four kittens on May 31, 2001. Backdating using a mean gestation of ninety-one days placed conception on or near March 1. The closest association to this date was with male M137 on March 10–12, although F106's association with M127 on March 13 also falls very close. If F106 conceived on March 10, the resulting gestation period would have been eighty-two days, the lower extreme for gestation lengths reported in other studies of wild and captive cougars across North America, which range from eighty-two to ninety-six days and average around ninety-one days (Rabb 1959; Anderson 1983; Beier and Barrett 1993; Logan and Sweanor 2001). Because of his dominant social status and pairing with F107 on March 10, male M137 seems the most likely sire of the litter.

## CHAPTER 16

### Dispersal and Population Change

Whether the goal is to recover, harvest, or restore wildlife populations, the vital rates presented in previous chapters are essential for making predictions about growth of populations. Population growth rate may then be used to predict how a management or recovery goal might affect growth and exchange between populations (McCullough 1996; Rabinowitz and Zeller 2010; Whittaker and Wolfe 2011; Newby et al. 2013). In this chapter we describe arrivals and departures of cougars through dispersal and discuss why PW and DW cougars might emigrate versus stay at home. Illuminating dispersal characteristics prior to and during wolf presence helps set the stage for understanding population growth and change of Northern Range cougars during our two study periods, which we address in the later sections of this chapter.

#### DEPARTURES AND ARRIVALS OF COUGARS VIA DISPERSAL

As yearling cougars matured, separated, and then remained separate from their mothers during subsequent locations within their natal area, we considered them to be on their own, or *independent*. By this time subadult cougars physically looked very similar to adults—young males at eighteen months of age could weigh 120 to 130 pounds, thus outweighing their mothers. After a typically short period of independence within or near their natal area—twelve to thirty-five days for Greater Yellowstone Northern Range offspring—most subadult cougars then began to travel through unfamiliar terrain in search of an area to establish and become a breeding adult [1]. Dispersal of cougars tended to include three stages: consistent movement away, or *emigration*, from the natal area, movement between the natal and a target or end area, and successful establishment, or *immigration*, into a new breeding site or home range (Bowler and Benton

2005; Newby et al. 2013). But the term *disperser* also included individuals that ultimately did not leave the natal area; that is, those that were philopatric. Thus the set of rules used to define dispersal influences whether individuals are considered emigrants or philopatric. Little overlap between old and new ranges can lead to classifying more individuals as emigrating dispersers in some study areas (Logan and Sweanor 2001; Creel and Creel 2002). We wondered, for example, whether a daughter or son in a new home range adjacent to but not overlapping the mother's home range was an emigrant from its natal area or was perhaps philopatric. If remaining in an adjacent yet non-overlapping home range confers similar reproductive and survival advantages to those of a home range that overlaps greater than 5 percent of one's natal area (see Logan and Sweanor 2001; Robinson and DeSimone 2011; Newby et al. 2013), should these individuals also be deemed philopatric?

We considered cougars to be philopatric when they were born in the study area and remained in it, either overlapping a portion of their natal area or establishing a home range within one home range diameter of the geometric center of their natal and established area [2]. We had few data to test differences in reproduction and survival of offspring overlapping versus those adjacent to their natal area, but their success appeared similar. Establishment within one home range diameter of the natal area should increase the odds that a daughter (or son) is familiar with local resources that provide reproductive and survival advantages. Yet by remaining so close, they might also breed with their father or mother. In studying black bears in New Mexico, Costello (2010) documented that virtually all female black bear offspring stayed near home—establishing within 0 to 5 km from their natal centers to new annual range centers.



An analysis of dispersal using genetic information may be the most appropriate way to evaluate effects of dispersal and could help standardize our view of dispersal and enhance understanding of its role during different periods of time and conditions (Biek et al. 2006c; Costello 2008, 2010). We collaborated on such an analysis to evaluate sex-biased dispersal using data between 1987 and 2003 and published results with Biek and colleagues (2006c), which we highlight later. In addition, to understand dispersal movements better and assess the contribution of dispersers to the surrounding area, we initiated a master's thesis study with cougar project technician Jesse Newby and collaborated on a larger study that assessed human-caused mortality on emigration, dispersal distance, and establishment success. These data were published in Jesse's thesis at the University of Montana and appear in journal articles by Newby and co-workers (Newby 2011; Newby et al. 2013).

As subadults dispersed from the Greater Yellowstone Northern Range, we followed their movements from the ground and with aerial telemetry flights ranging up to 200 km from the primary study area. As the young cats moved farther from the study area, it became more difficult to locate them and to obtain detailed information on their movements and their fates. For eleven of twenty-one emigrants prior to wolves and nineteen of thirty emigrants during wolf restoration, we obtained information on dispersal distances and fates of the cats from hunter tag returns. We recorded dispersal distance for twenty-two and twenty-seven individuals in the PW and DW studies, respectively. We used two measures for dispersal distance: (1) the linear or Euclidean distance between a disperser's origin and final dispersal location and (2) a scaled measure of dispersal distance based on the average home range diameter of resident adult cougars (see Newby et al. 2013).

## INDEPENDENCE, PHILOPATRY AND EMIGRATION OF SUBADULTS

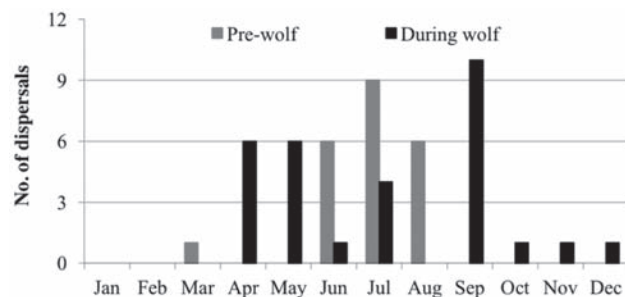
When movements of radio-collared subadult females localized and reflected site fidelity by the time they were twenty-four months old or older, we deemed them to be philopatric or considered them successfully emigrated (Murphy 1998; Logan and Sweanor 2001; Cooley et al. 2009). We defined age at emigration as a young cougar's first movement beyond its natal area that was followed by continuous movement greater than one home range diameter from the geomet-

ric center of the natal area. Male dispersal was more complicated because of males' tendency to restrict movements during their first winter after leaving their natal range. If they survived their first winter, subadult males often abandoned temporary winter ranges and continued dispersal movements to another location (Beier 1995). Consequently, we assumed that males were still transient until the beginning of autumn (September 23) following their first winter independent from their mothers (Newby et al. 2013). Subadults that could not be reliably relocated using radio-telemetry but were later relocated from the return of ear tags from hunters were considered successful dispersers if they were older than twenty-four months for females and thirty months for males. If they were killed at ages younger than this, we considered their dispersal to have been unsuccessful. New individuals that originated from elsewhere outside the study area and established home ranges were deemed immigrants that entered the resident adult portion of the population (Logan and Sweanor 2011).

## Age of Independence and Dispersal

The mother is likely the main motivator encouraging her young to depart (Seidensticker et al. 1973; Beier 1995), and dispersal of self-sufficient offspring may benefit her, as the timing of when offspring depart should also confer advantages to the mother and her offspring. The timing of independence and then departure of young on the Northern Range coincided with snow-free months and the birth of elk calves and deer fawns in June and July (fig. 16.1). Other small prey, such as ground squirrels, were also available as they emerged from hibernation in late April and May with another peak in activity in fall as they gathered food for the approaching winter. Encountering easily catchable prey should enhance the survival of young cougars still honing hunting skills as they move through unfamiliar terrain.

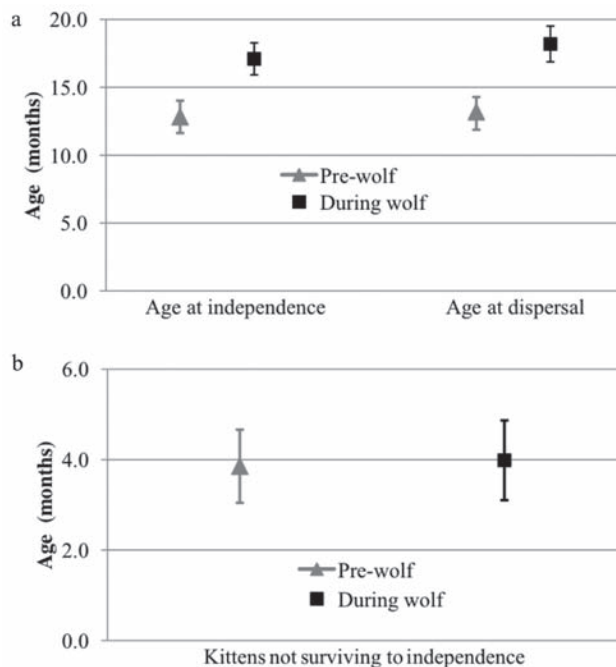
Compared to the PW situation with fewer competitors, we expected that kittens should become independent and disperse earlier if resources became limited from competition with wolves and bears and there was little room to accommodate offspring. Ending maternal care of offspring that no longer needed it would enable the adult female to devote her energy to obtaining resources for raising a new litter (Logan and Sweanor 2010: 108). Instead, kittens became independent and dispersed from their mothers at approximately five months older during wolf presence (fig. 16.2). Age



**FIGURE 16.1.** During their second year of life, offspring dispersed from their natal area primarily during summer months on the Greater Yellowstone Northern Range, 1987–2005. While the mother may encourage her young to leave, timing of dispersal coincided with snow-free months, the birth of elk calves and deer fawns in June and July, and increased availability of small prey such as ground squirrels, which emerge from hibernation in spring. PW  $n = 22$  dispersers; DW  $n = 29$  dispersers.

at independence averaged  $12.8 \pm 3.4$  months ( $n = 27$ ) during the PW study and  $17.1 \pm 3.2$  months ( $n = 29$ ) after wolf restoration [3]. Prior to wolves, offspring dispersed at a younger average age of  $13.2 \pm 2.6$  months ( $n = 22$ ) than the average age offspring dispersed after wolf restoration— $18.4 \pm 3.4$  months ( $n = 25$ ) [4]. While these ages of dispersal are typical of those reported in at least seven other studies—ranging from 11 to 23 months of age—we encountered no other study that compared dispersal ages during two different time periods or differing environmental conditions (Hemker et al. 1984; Maehr et al. 1991; Ross and Jalkotzy 1992; Beier 1995; Logan and Sweanor 2001).

Although DW subadults dispersed at older ages, there was little difference in the proportion of subadult females and males dispersing or emigrating from the study area during wolf restoration as compared to the PW period [5]. Prior to wolf restoration, 17 subadult females and 12 subadult males survived to begin their dispersal. Of these, 6 females and 1 male were philopatric. Another 11 females and 10 males emigrated from the study area. During wolf restoration, 18 subadult females and 21 subadult males survived to begin their dispersal. Of these, 2 females and 2 males were philopatric, whereas another 14 females and 16 males emigrated from the study area. The remainder of individuals, 1 male prior to wolves and 2 females and 4 males during wolf restoration, either died or had a radio collar malfunction prior to successful emigration.



**FIGURE 16.2.** Mean ages (95% confidence interval error bars) of kittens at independence from their mothers and dispersal from their natal area (a). Kittens became independent and dispersed from their mothers and at approximately five months older during wolf presence compared to prior to wolves. This change was not the result of a difference in kitten age at death (b). PW independence  $n = 27$ ; DW independence  $n = 29$ ; PW dispersal  $n = 22$ ; DW dispersal  $n = 25$ ; PW age at death  $n = 33$ ; DW age at death  $n = 20$ .

### Philopatry

Between 1988 and 1991, 35 percent of PW subadult females—6 subadult females from 6 different mothers—settled near their mothers. Four of these females overlapped between 35 percent and 100 percent of their natal area. We were unable to calculate a home range for the other 2 females because of too few locations, but they established within 4 to 8 km from the edge of their natal area. Subadult male M38 also remained, establishing a home range within 6.2 km from the edge of his natal area, where he remained at the end of the PW study.

In the DW study we documented fewer philopatric females—2 non-related females, F101 and F102, stayed near home. Two non-related males, M127 and M170, also stayed (see text box 16.1). This equated to 11 percent of females and 10 percent of males remaining near their natal area. Female

F102 became independent of her mother at about 21 months of age and established a home range overlapping 20 percent of her natal area by late summer 2000. Female F101 became independent of her mother when she was about 20 months old and eventually established her home range within 4.8 km from the edge of her natal area. Three of these 4 individuals established ranges before wolves were fully restored in 2002–3.

Philopatry of female cougar progeny is common, with 41 percent to 67 percent of female offspring establishing near their natal area (Logan and Sweanor 2001; Robinson and DeSimone 2011). The philopatry of male offspring that we observed appears to be exceptional compared to other studies (see Logan and Sweanor 2010). Males remaining near their natal areas have been documented only in Florida and Southern California, where their dispersal was frustrated by urban development and agriculture as well as territories occupied by other males (Beier 1995; Maehr 1997a). In both those study areas, subadult males attempted to disperse and, if not killed by other males or vehicles, returned to the vicinity of their natal area, although most attempted to disperse again.

Of course, our definition of philopatry differed somewhat from that in other cougar studies, thus including 1 male prior to wolves and 1 male during wolf restoration that would be considered emigrants when using stricter conditions of overlap with the natal area. Even so, male M127 clearly remained in his natal area and became a successful breeding adult. Because evidence in the literature supports male dispersal primarily to avoid inbreeding, our observations raise the question: Why should some males stay at all, particularly during greater competition for resources? We address this question later in the chapter.

## Emigration

Before wolves settled, approximately 65 percent of PW subadult females and 78 percent of PW subadult males successfully departed from the study area. Following wolf restoration, an increased proportion of females and a similar proportion of males departed from the study area—78 percent of DW females and 76 percent of DW males. This equated to about 3.0–3.7 emigrants per year over a span of seven years prior to wolves and 3.7–4.4 emigrants per year over a span of seven years during wolf restoration [6]. In a basin and range desert environment, emigration rates of 5.3 to 8.5 emigrants per year were almost double those of Greater Yellowstone cougars (Logan and Sweanor 2001: 153). In total, 25 of 35 subadult

females (71%) and 26 of 33 subadult males (79%) emigrated during the course of our studies, but not all of them survived to establish home ranges elsewhere.

As cougars emigrated from the Greater Yellowstone Northern Range study area, they encountered mostly public lands. Many moved through national forests and wilderness to the north of the Yellowstone boundary. If they survived their first winter outside these protected areas, 13 percent then traveled south to Grand Teton National Park; Jackson and Lander, Wyoming; and near Grays Lake National Wildlife Refuge in Idaho. We “censored,” or removed, 11 PW subadult cougars and 21 DW subadults that died in the process of dispersal or with which we lost contact after their leaving. Altogether, 64 percent (1 female and all 6 males) of successful PW emigrants were eventually killed during hunting seasons, with 1 male surviving to 67.4 months old. During wolf restoration, 86 percent (all 6 females and 6 of 8 males) of successful emigrants died during hunting seasons at mean ages of 52.5 months for females and 36.5 months for males.

After we censored cougars that died, we found that similar proportions of subadult females and males survived to ages where they appeared to be establishing home ranges [7]. Because these subadult females survived to similar ages and the males also survived to similar ages, we pooled females and pooled males across the two study phases and then compared differences between the sexes. Females that were successful emigrants survived to an older median age of 55.8 months than the median age of 31.7 months emigrating males reached [8]. When we removed 8 of the 12 males because they died at around 30 months of age, the point when we considered them established, males survived to the same ages as females—50.2 and 55.8 months, respectively [9]. Males that died at around 30 months were killed by hunters.

Females and males moved similar absolute distances (Euclidean distance) to the areas where they established—females moved a median of 45.4 km (mean = 70.4 km) and males moved a median of 69.6 km (mean = 70.0 km). But after we scaled dispersal distances by average home range diameters, Northern Range subadult females moved farther than Northern Range subadult males and farther than subadults in another, more heavily hunted study area in the Garnet Hills of Montana (Newby et al. 2013: fig. 1). The absolute distances moved by Northern Range emigrants—both females and males—were on the lower end of average dispersal distances of male cougars, which ranged from about

49 to 483 km in eight studies across the western United States and Canada (Logan and Sweanor 2000; Laundré and Hernández 2003). Although survival success to move longer distances may be rare, 1 male that departed from the Black Hills of South Dakota moved as far as 1,067 km east, and 1 female that left Utah ended up in Colorado after traveling a total distance of 1,341 km (Thompson and Jenks 2005; Stoner et al. 2007).

### WHY SHOULD MOTHERS SUPPORT OFFSPRING LONGER IN A RISKIER ENVIRONMENT?

Older, more experienced mothers living in a riskier environment with wolves and bears reared offspring longer before the youngsters became independent and dispersed. But why should females allow energetically costly young to remain longer when competition for resources and risk of encounter with competitors were greater? We consider two indirect explanations for lower maternity rates that seem possible, although non-exclusive of each other: (1) density dependence and habitat quality and (2) experience and protection provided to young.

In an initially low-density and growing cougar population when resources were abundant and competitors were few, such as in the PW period, a female cougar might invest in producing more offspring in a shorter amount of time because the odds of her offspring establishing in good-quality habitat were high, particularly for daughters. By staying at home, philopatric daughters not only remained in good-quality habitat where they were familiar with prey and escape features, they also tended to breed and have first litters more quickly (Julliard 2000; Logan and Sweanor 2001). Investing in producing more offspring, particularly more female offspring when conditions are good, should result in increased reproductive success and inclusive fitness. However, the landscape became riskier as wolves were restored within the study area and grizzly bear numbers increased. Home ranges of cougars were also limited, and fewer elk were available. A mother supporting young longer in a lesser-quality environment with few places for establishment would enable her young to grow larger and also more experienced with prey capture and competitors. Such experience should enhance subadult survival and success of establishment following dispersal. Kitten survival was enhanced during wolf presence as compared to the PW period, not only as a result of greater

stability in male territories but because cougar mothers provided for offspring for an average of five months longer. Once they became independent from their mothers and preceding their departure from the study area, subadult females had similar rates of survival prior to (0.83, SE = 0.015) and during (0.80, SE = 0.048) wolf restoration. Subadult males also had similar rates of survival prior to departing from the study area—0.67 (SE = 0.065) for PW males and 0.61 (SE = 0.142) for DW males—although their survival was lower than that of subadult females (see fig. 15.6).

In addition to longer stays providing benefits to the offspring, mothers themselves might obtain group-related benefits from their association with large, more experienced offspring, benefiting from having “many eyes” to detect the wolves and bears that were more frequent visitors to kills made by maternal females (Elgar and Catterall 1981; Elgar 1989). While increased competition for food and costs to the family group would suggest selection against sharing kills with other individuals as they grow, sharing with offspring or other mature females could also benefit the entire group in terms of reduced individual vigilance and intimidation of competitors. Vigilance has been found to rise with age in various species, but we knew of no studies that investigated the effect of age on cougars—probably because they are difficult to observe (Sullivan 1988; Boinski and Fragarzy 1989; Caro 1994). Just as young cheetah kittens failed to recognize danger and generally scattered when the mother ran (Caro 1994), on the few occasions when we observed family groups at kills, their behavior suggested that young kittens were less vigilant about their surroundings than were their mothers. Even during travel, we detected young kittens romping in snow as they moved alongside their mother. The burden of detecting danger—other carnivores or adult male cougars—likely falls mostly on the mother until kittens reach a certain age, indicating that an important aspect of maternal care is predator detection (Caro 1994). As kittens age and gain experience, they may spend a greater proportion of time alert to danger.

A group of similar-size cougars may also provide anti-predator benefits through intimidation of other carnivores. We and others have now documented maternal females and kittens sharing kills with yearling females of unknown relationship (K. Logan, pers. comm., 2011; H. Quigley, pers. comm., 2011). These groups may be less likely to be approached by wolves, bears, or male cougars than are sin-



gle cougars. Such behaviors have been observed in cheetahs, where offspring ten months old and older showed a level of vigilance approaching that of adult cheetahs (Caro 1994). In addition, cheetah mothers in the company of older kittens were somewhat less vigilant during the midday rest period than were lone adult females. Finally, single adolescent cheetahs were also more likely to be approached by spotted hyenas and male cheetahs than were groups of adolescents.

### **ADAPTIVE SIGNIFICANCE OF TIMING OF INDEPENDENCE, DISPERSING, OR STAYING**

Long-distance dispersal from the birth area is an intrinsic and important aspect in the ecology of carnivore populations (Chepko-Sade and Halpin 1987; Sweanor et al. 2000; Clobert et al. 2001; Frank and Woodroffe 2001). Theoretically, it is adaptive, as it should lead to increased individual reproductive success (Morris 1982). But why did some cougars successfully remain while others departed from the study area? In particular, because male-biased dispersal is common in solitary carnivores, why should any males be philopatric (Waser and Jones 1983)? Decisions on whether to stay at home or leave are hypothesized to be driven by three main factors: competition for mates, competition for food and space, and inbreeding avoidance (Greenwood 1980). We briefly delve into these factors, as more than one factor may motivate dispersal in a given individual (Dobson and Jones 1985; Waser 1985; Creel and Creel 2001; Logan and Sweanor 2001).

#### **Competition for Mates**

In the polygynous mating system common in mammals, competition for mates may be especially intense among males (Dobson 1982). In cougar populations protected from human hunting and development, young, less experienced males should commonly disperse, as competition for limited breeding opportunities is intense. Yet once they depart from the natal area, independent subadults may navigate through habitats with greater risks than those faced by adults or those subadults that stay behind. As they travel in unfamiliar landscapes, subadults must balance costs of foraging with risks of encounter with interspecific competitors, humans, and conspecifics; and dispersers generally have higher rates of mortality than non-dispersers that stay near home (Waser 1985; Waser et al. 1994; Beier 1995; Ruth et al. 1998; Heithaus and Dill 2002). Although localized loss of mature males from hunting or other human-caused mortality encourages

immigration of young males, these same immigrants may be removed through hunting around the time they are first breeding (Robinson et al. 2008; Cooley et al. 2009; Costello 2010; Robinson and DeSimone 2011). This could also partially explain why Greater Yellowstone subadult males did not disperse as far as dispersing subadult female cougars.

If they survive the various hazards of dispersing, by the time they find a vacant area, immigrant males should have the experience and physical attributes to compete more readily for a mate (Logan and Sweanor 2001). Yet competition for mates does not fully explain dispersal in males on the Greater Yellowstone Northern Range because males dispersed equally during the PW period, when available mates and male competitors were fewer and of similar age, as they did during wolf restoration. Other studies have found this pattern as well—male cougars disperse independent of the density of resident adult males (Logan and Sweanor 2001). Although females generally do not compete with other females for mating opportunities through fighting, and more females remained when food was abundant prior to wolves, 65 percent still emigrated. Perhaps selection to escape from reproductive suppression also plays a role for females, but substantially less than the competitive forces exerted on young males.

#### **Competition for Food and Space**

Competition for food rather than mates should also influence dispersal, but pressure on males and females to disperse should be more equal (McNutt 1996). Dispersal patterns of subadult females are thought to be partially density-dependent (Beier 1995; Logan and Sweanor 2001, 2010). If so, as more Northern Range female cougars competed for food and other resources, young females should have been more likely to establish ranges apart from their natal range. This appeared to be the case during wolf restoration, when fewer females remained and slightly more—78 percent—emigrated. During the PW study, when cougar density was lower and elk numbers were increasing, subadult females benefited by quickly settling adjacent to their mothers. Then mothers willing to share resources with daughters increased their inclusive fitness as well because not only were philopatric daughters familiar with resources, but they also might breed and have first litters more quickly (Julliard 2000; Logan and Sweanor 2001). And by staying near home, philopatric daughters ensure that good-quality territories will

remain in the family for at least some time. In the DW period it became more difficult for young females to settle, as the study area filled up with other cougars, the elk population declined, and less space to establish was available as the numbers of wolves and bears increased in the study area. Under this scenario, emigration costs were probably less than the costs of philopatry because emigration enabled individuals to exploit habitats with less competition and perhaps more abundant resources compared to the natal area (Logan and Sweanor 2010).

Similar to PW females, there was adequate space and food for PW male offspring, and fewer dominant carnivore competitors were present. Yet 83 percent of PW male progeny emigrated, similar to 76 percent of DW male progeny that emigrated during wolf restoration, suggesting that like competition for mates, competition for food does not fully explain dispersal in males.

When combining males and females that emigrated, we found some indication that emigration tendencies were greater in the presence of a resident wolf population than they were in places with fewer wolves (see Newby et al. 2013). Because cougars showed avoidance of wolves and situated their core areas away from core areas of wolves, fewer home ranges might have been available for cougars to establish than if wolves were not present (chapters 10 and 11). Although we did not yet find food to be limiting for resident individuals, cougars competed with wolves and bears for space and for live and dead prey, and there were fewer opportunities for offspring to establish than during the PW period. Given that intra- and interspecific competition reduced available territories and prey were less available during wolf restoration, what were the advantages of a few young males establishing territories overlapping or adjacent to natal areas? Perhaps when conditions away from home are as risky for establishment as they are near home and room to establish a territory exists, young males may occasionally stay. The ability to perceive information about conspecific density and habitat quality in both the natal and surrounding patches should have large evolutionary benefits (Bach et al. 2007; Enfjäll and Leimar 2009). After first testing conditions near his natal area and then beyond when he traveled north and spent time in the Boulder River, philopatric male M127 was possibly able to evaluate risks of dispersal relative to staying at home. After potentially encountering unfavorable conditions, he returned and overlapped with M137. The older

male seemed to tolerate his presence for roughly thirty-one months before M137 died. Male M127 quickly established in the vacant territory that overlapped his natal area.

### Avoiding Inbreeding

Over time, mating with close relatives can eventually reduce the fitness of individuals and increase extinction risk of populations, as evidenced by the reduced genetic variation and increased deleterious effects—poor semen characteristics and high rate of heart defects—in the Florida panther (O'Brien et al. 1990; Roelke et al. 1993; Hedrick 1995; Culver et al. 2000). Dispersal, then, reduces the frequency of close inbreeding to very low levels in some carnivores (Pusey and Packer 1987; Ralls et al. 1988). The fact that ten females but only three males that were born on the Greater Yellowstone Northern Range also became residents there clearly underlines greater female fidelity to the natal area than male fidelity, as described for cougars elsewhere (Logan and Sweanor 2001; Robinson and DeSimone 2011). Because sharing resources with daughters confers advantages to females, male dispersal would reduce the chances of close inbreeding.

Genetic data from our study revealed patterns consistent with males generally immigrating from outside the Northern Range, perhaps over distances upward of 1,341 km, as has been documented in male cougars (Stoner et al. 2007). Resident male cougars typically carried alleles that were not shared with other males and that were uncommon in the Northern Range (Biek et al. 2006c). Resident males also shared few alleles with previous female residents, including those with high reproductive success (Biek et al. 2006c). While these genetic analyses occurred before philopatric male M127 and M170 became reproductively active in the DW study, we did not expect the outcome of the genetic analyses to have changed much during subsequent years. The majority of DW males were immigrants, although they immigrated at about half the rate—0.9 per year—compared to the PW period (1.7 per year). Although male philopatry might increase the likelihood of close inbreeding, parents that die before their offspring reach breeding age would alter the probability that parents and offspring might breed (Creel and Creel 2002).

Not only were female cougars more similar to one another genetically than were males, but offspring of PW female cougars were related to DW females ( $R = 0.819$ ; Biek et al. 2006c: fig. 2a). Two females, philopatric F17 and F53, were still

present as resident females as our DW study began, surviving until 2002 and 2004, respectively. Some of their daughters may have established between 1994 and 1998 when we were not studying Yellowstone cougars. Although there was a genetic legacy between study phases, contemporary residents and female residents separated by few generations were mostly unrelated—they did not share more alleles on average than would be expected by chance (Biek et al. 2006c). The arrival of new immigrant males may be sufficient to introduce new alleles and reduce levels of allele sharing among females. Further, our genetic results suggested that dispersal distances in female cougars were generally large enough to reduce the chance of interaction among relatives. When we factored out the females that stayed, females that did leave moved a greater number of home range diameters away than did subadult males that emigrated (Newby et al. 2013).

In summary, resident males apparently originated in areas that were geographically distant enough to exhibit pronounced genetic differences, supporting the notion that inbreeding avoidance may represent the most important adaptive advantage of long-distance dispersal in male cougars (Pusey 1987; Logan and Sweanor 2001; Biek et al. 2006c). Although females did not emigrate as consistently as did subadult males, emigration by both sexes reduced the odds of inbreeding. Yet emigration of female offspring was also at least partially density-dependent, as there was little room to accommodate philopatry or immigration of young cougars in the carnivore-rich environment during wolf restoration as compared to the PW period. Unlike among females, male dispersal was not related to density, but there was still pressure to leave from competition with older, dominant males. The philopatry of male offspring that we observed appears to be exceptional compared to other studies, but perhaps it resulted from the ability of dispersers to perceive information about conspecific density and habitat quality in both the natal area and surrounding patches they investigated during excursions.

## POPULATION GROWTH BEFORE AND DURING WOLF RESTORATION

We used our end-of-winter point estimates, including back-logging individuals into the population, to estimate the number, density, and growth rates of cougars prior to and during wolf presence. Prior to wolf restoration, the number and density of cougars residing on the Greater Yellowstone Northern

Range increased. In the early years following wolf restoration, the population grew, and a greater number of cougars was present than prior to wolf restoration. However, the growth was not sustained in the later years of our DW study.

## Density Estimates

In tables 16.1 and 16.2 we provide estimates of cougar density across winters for three defined areas: (1) the northern ungulate winter range of approximately 662 km<sup>2</sup> as presented by Murphy (1998), (2) the area defined by the winter 95 percent synoptic habitat model for each study period (chapter 11), and (3) the area represented by the 95 percent fixed kernel utilization distribution (chapter 11). Cougar numbers within the area defined by the ungulate winter range reflect an overestimate of density, as we did not make proportional adjustments for cougars that overlapped the boundary but may have used the area very little. We provide it for reference following estimates in Murphy (1998). Density estimates based on the 95 percent synoptic habitat model and on the 95 percent fixed kernel reflect minimums. While we feel that the 95 percent synoptic model should provide the closest approximation of density, as the area was strongly tied to habitats used by cougars, the three estimates highlight some of the difficulties when comparing density between study areas (Maletzke 2010; Quigley and Hornocker 2010; Beausoleil et al. 2013).

When using the synoptic habitat area, the density of cougars across years prior to wolf restoration averaged 0.95 resident adults per 100 km<sup>2</sup> and a total density averaging 1.6 cougars per 100 km<sup>2</sup>. Following wolf restoration, the density of cougars across years doubled—averaging 2.0 resident adults per 100 km<sup>2</sup> and a total density averaging 3.9 cougars per 100 km<sup>2</sup>. In the western United States and Canada, where long-term cougar research has been conducted, densities averaged 1.6 resident adults per 100 km<sup>2</sup>, and total densities (including kittens and subadults) averaged 2.6 cougars per 100 km<sup>2</sup> (Quigley and Hornocker 2010: 70, table 5.2; Beausoleil et al. 2013). Relative to these other studies available for comparisons, our study area received little hunting pressure, and the doubling in density between PW and DW periods initially suggests that cougars were not limited by wolves or bears.

Our estimates provide some measure of cougar density from a defined area, but they do not link density with habitat quality across the landscape. Hence we integrated the density of cougars with our winter synoptic habitat maps and then summed across all adult cougars for two specific time

**TABLE 16.1.** Estimated density (per 100 km<sup>2</sup>)<sup>a</sup> of cougars each April prior to wolf restoration on the Greater Yellowstone Northern Range, 1987–93.

| Winter of Estimate | Total Cougars <sup>b</sup> | Winter Range Core<br>662 km <sup>2</sup> | Winter 95% Synoptic HR<br>1,424 km <sup>2</sup> | Winter 95% FK HR<br>2,203 km <sup>2</sup> | Total Adults <sup>b</sup> | Winter Range Core<br>662 km <sup>2</sup> | Winter 95% Synoptic HR<br>1,424 km <sup>2</sup> | Winter 95% FK HR<br>2,203 km <sup>2</sup> |
|--------------------|----------------------------|------------------------------------------|-------------------------------------------------|-------------------------------------------|---------------------------|------------------------------------------|-------------------------------------------------|-------------------------------------------|
| 1987–88            | 15 (15)                    | 2.27                                     | 1.05                                            | 0.68                                      | 9 (10)                    | 1.36                                     | 0.70                                            | 0.45                                      |
| 1988–89            | 16 (17)                    | 2.42                                     | 1.19                                            | 0.77                                      | 9 (12)                    | 1.36                                     | 0.84                                            | 0.54                                      |
| 1989–90            | 18 (26)                    | 2.72                                     | 1.83                                            | 1.18                                      | 7 (12)                    | 1.06                                     | 0.84                                            | 0.54                                      |
| 1990–91            | 20 (29)                    | 3.02                                     | 2.04                                            | 1.32                                      | 9 (14)                    | 1.36                                     | 0.98                                            | 0.64                                      |
| 1991–92            | 22 (30)                    | 3.32                                     | 2.11                                            | 1.36                                      | 10 (15)                   | 1.51                                     | 1.05                                            | 0.68                                      |
| 1992–93            | 17 (18)                    | 2.57                                     | 1.26                                            | 0.82                                      | 12 (18)                   | 1.81                                     | 1.26                                            | 0.82                                      |

<sup>a</sup> Estimates included marked and unmarked cougars known to be present in a given winter. Winter range core = the well-defined, fixed boundary ungulate winter range; winter 95% synoptic HR = area used by all adult cougars based on our synoptic home range modeling in chapter 11; winter 95% FK HR = fixed kernel home range area estimated from winter locations of all adult radio-collared cougars.

<sup>b</sup> Estimated total number of cougars included adult females, adult males, subadult females, subadult males, and kittens within Yellowstone National Park, Bear Creek, and Trail Creek. Numbers in parentheses are minimum estimates for the entire study area, including Cinnabar Creek and Dome Mountain to the north of Yellowstone National Park. Density estimates for the 95 percent synoptic and the 95 percent fixed kernel home range areas include minimum estimated number of cougars within the two areas (number in parentheses).

**TABLE 16.2.** Estimated density of cougars each April during wolf restoration on the Greater Yellowstone Northern Range, 1998–2005.

| Winter of Estimate | Total Cougars <sup>b</sup> | Density Estimates (per 100 km <sup>2</sup> ) <sup>a</sup> |                                               |                                           |              |                                          |                                               |                                           |
|--------------------|----------------------------|-----------------------------------------------------------|-----------------------------------------------|-------------------------------------------|--------------|------------------------------------------|-----------------------------------------------|-------------------------------------------|
|                    |                            | Winter Range Core<br>662 km <sup>2</sup>                  | Winter 95% Synoptic HR<br>816 km <sup>2</sup> | Winter 95% FK HR<br>1,709 km <sup>2</sup> | Total Adults | Winter Range Core<br>662 km <sup>2</sup> | Winter 95% Synoptic HR<br>816 km <sup>2</sup> | Winter 95% FK HR<br>1,709 km <sup>2</sup> |
| 1998–99            | 34                         | 5.14                                                      | 4.17                                          | 1.99                                      | 13           | 1.96                                     | 1.59                                          | 0.76                                      |
| 1999–2000          | 30                         | 4.53                                                      | 3.68                                          | 1.76                                      | 15           | 2.27                                     | 1.84                                          | 0.88                                      |
| 2000–2001          | 42                         | 6.34                                                      | 5.15                                          | 2.46                                      | 19           | 2.87                                     | 2.33                                          | 1.11                                      |
| 2001–2             | 26                         | 3.93                                                      | 3.19                                          | 1.52                                      | 18           | 2.72                                     | 2.21                                          | 1.05                                      |
| 2002–3             | 26                         | 3.93                                                      | 3.19                                          | 1.52                                      | 17           | 2.57                                     | 2.08                                          | 0.99                                      |
| 2003–4             | 32                         | 4.83                                                      | 3.92                                          | 1.87                                      | 15           | 2.27                                     | 1.84                                          | 0.88                                      |

<sup>a</sup> Estimates included marked and unmarked cougars known to be present in a given winter. Winter range core = the well-defined, fixed boundary ungulate winter range; winter 95% synoptic HR = area used by all adult cougars based on our synoptic home range modeling in chapter 11; winter 95% FK HR = fixed kernel home range area estimated from winter locations of all adult radio-collared cougars.

<sup>b</sup> Total number of cougars included adult females, adult males, subadult females, subadult males, and kittens.

frames [10]. We mapped cougar density for winter 1991–92 of the PW period and winter 2000–2001 of the DW period, as these time periods reflected periods with the most information for cougars and when the greatest proportion of cougars was marked (fig. 16.3a, 16.3b).

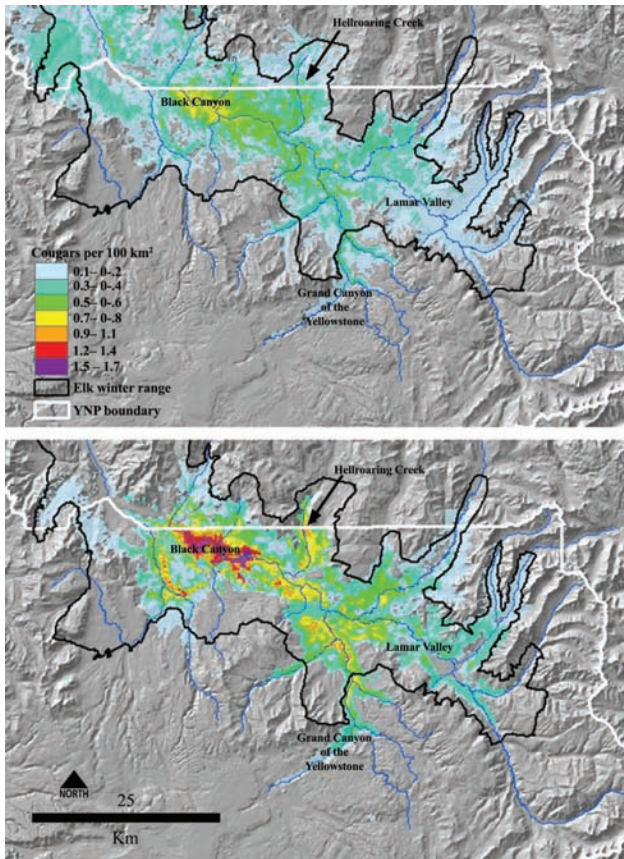
As shown in figure 16.3b, cougar density along the Grand Canyon of the Yellowstone River, the rocky outcrops along Hellroaring Creek, and along the Black Canyon of the Yellowstone River increased compared to the PW period (fig. 16.3a). This increased density of adults primarily resulted from cougars avoiding areas frequented by wolves during winter and again reflects forested, rocky terrain providing refuge from risk of competition with wolves. Because some once suitable habitats were no longer used by cougars, the similar

to slight increase in density runs counter to the prediction of a lower cougar density when sympatric with wolves.

## Population Growth

We determined observed growth rates prior to and during wolf restoration from annual counts of collared and unmarked cougars. In addition, we estimated population growth by constructing a post-breeding, female-based, age-classified *matrix model* using the vital rates from chapters 14 and 15 (Caswell 2001; Mills 2007). To estimate population growth rates ( $\lambda$ ) during the PW and DW studies, we used the finite rate of increase function in the PopTools extension for Microsoft Excel (PopTools version 3.0.5, [www.cse.csiro.au/poptools](http://www.cse.csiro.au/poptools), accessed June 20, 2008). We used study





**FIGURE 16.3.** The relative density of adult cougars (cougars per 100 km<sup>2</sup>) during winters 1991–92 prior to wolves (a) and 2000–2001 during wolf restoration and colonization (b) on the Greater Yellowstone Northern Range, Montana and Wyoming. One female known to be present but unmarked (a) and one male known to be present but unmarked (b) are not included. Estimated density at the northern periphery outside Yellowstone National Park (boundary in white) is more tenuous, as winter range extends farther to the north, yet our field research efforts were limited, and unmarked cougars likely overlapped on the northern periphery shown. Deep snow and lack of prey outside the elk winter range boundary (black line) within Yellowstone National Park limit cougars to areas shown. While still considered a minimum estimate, we considered cougar density within the park reliable, as 87 percent to 94 percent of cougars were marked during the time frame shown.

phase-specific maternity rates ( $m_x$ ) and age-specific survival estimates for females from birth (age class zero) to age fourteen as matrix inputs (Ruth et al. 2011). Because the simple deterministic models we used assumed a closed population structure (i.e., no immigration or emigration), we adjusted

survival rates for yearling females based on our estimates of immigration and emigration. To determine which age classes and vital rates had the largest contribution and influence on the growth of the population, we used PopTools to evaluate the sensitivity and elasticity of  $\lambda$  to changes in age-specific survival and reproductive rates (Caswell 2001). In addition, we estimated the annual per capita contribution ( $C'$  following Runge et al. 2006) of the PW and DW study populations to growth in the landscape surrounding the Greater Yellowstone area (Newby et al. 2013). The contribution of each population was determined by accounting for both recruitment of philopatric individuals into the population and recruits provided to other subpopulations via successful emigration.

Prior to wolf restoration, the cougar population grew relatively rapidly—from 9 percent to 25 percent, depending on the metric of cougar population growth (range for 95% CIs; table 16.3) [11]. Coincident with the absence of wolves during the years 1987 to 1994, elk population rapidly increased after the 1988 fires, elk calves were abundant, and the environment was ripe for cougars to grow in number. Although kitten survival rates were low, the reproductive rate of female cougars was consistent, and population growth occurred as a result of philopatry within the study population as well as new arrivals from other areas. Following the arrival of wolves, the cougar population declined at between 3 percent and 17 percent, depending on the metric used (table 16.3). In the early years following wolf restoration, the cougar population initially continued to grow at upward of 10 percent between 1998 and 2001. This changed during 2002 through the end of our study, when the wolf population reached peak numbers, elk numbers began to fall, and cougars avoided wolves. During peak wolf numbers the cougar population was in decline by as much as 13 percent to 22 percent, which did not include 2005, as our field efforts wound down and we were unable to keep tabs on cougar numbers across the study area.

Cougars expended energy defending kills from wolves and bears and territories from conspecifics. Such energy expenditure and the reduced availability of prey should reduce the local carrying capacity for solitary cougars and may partially explain slowed population growth and then decline as our study progressed. But the decline was confounded by other factors. The cougar population during wolf presence exhibited overall static density in the adult segment until the final years of our study, when deaths from encoun-

**TABLE 16.3.** Estimates of cougar population growth, immigration, emigration, recruitment to the population, and annual contribution of individuals to surrounding areas prior to and during wolf restoration on the Greater Yellowstone Northern Range, 1987–2005.

| Study Phase                 | Geometric Population Growth | Age-Structured Matrix | Population Contribution Estimates (95% CI) <sup>a</sup> |                      |                     |                      |                      |
|-----------------------------|-----------------------------|-----------------------|---------------------------------------------------------|----------------------|---------------------|----------------------|----------------------|
|                             | <i>r</i> (95% CI)           | $\lambda$ (95% CI)    | $\lambda$                                               | Recruitment          | Contribution        | Immigration          | Emigration           |
| PRE-WOLF                    |                             |                       |                                                         |                      |                     |                      |                      |
| Adults                      | 0.12<br>(0.09, 0.15)        |                       |                                                         |                      |                     |                      |                      |
| All cougars                 | 0.17<br>(0.10, 0.25)        | 1.12<br>(1.04, 1.17)  | 1.11<br>(1.03, 1.18)                                    | 0.98<br>(0.92, 1.03) | 1.1<br>(0.96, 1.23) | 0.14<br>(0.08, 0.20) | 0.17<br>(0.03, 0.31) |
| DURING WOLF                 |                             |                       |                                                         |                      |                     |                      |                      |
| Adults early<br>(1998–2001) | 0.09<br>(-0.03, 0.21)       |                       |                                                         |                      |                     |                      |                      |
| Adults late<br>(2002–5)     | -0.13 (-0.21, -0.04)        |                       |                                                         |                      |                     |                      |                      |
| All cougars                 | -0.03<br>(-0.15, -0.10)     | 0.83<br>(0.78, 0.87)  | 0.95<br>(0.84, 1.06)                                    | 0.88<br>(0.85, 0.94) | 1.05<br>(0.95–1.15) | 0.05<br>(0.01, 0.09) | 0.23<br>(0.13, 0.33) |

<sup>a</sup> Estimates of  $\lambda$ , recruitment, immigration, emigration, and contribution to surrounding areas are from Newby et al. (2013).

ters with wolves, disease, and unexplained natural mortality were not replaced by new individuals at the time our study ended. Although the population initially increased and then declined, the population continued to be a net exporter of emigrants and experienced a low per capita immigration rate of 0.05, likely because there was little room for new immigrants to establish (table 16.3; Newby et al. 2013).

Overall, population growth in our studies, averaging 12 percent during population rebuilding, was similar to lightly hunted populations elsewhere and mirrored growth rates of 14 percent observed in several study areas in Washington after hunting mortalities were removed (table 16.4; Beausoleil et al. 2013; Wielgus et al. 2013). Sensitivity and elasticity analyses revealed that the growth rate of cougars prior to and during wolf restoration was most sensitive to changes in adult female survival (Ruth et al. 2011). Prior to wolves the restoring population relied on female survival contributing to population growth slightly more than did the DW study population. Although adult female survival typically exerts the most influence on population growth in many long-lived species, accounting for dispersal and immigration in our matrix models indicated that kitten and subadult survival followed in importance (Gaillard et al. 1998; Biek et al. 2006b; Lambert et al. 2006; Robinson and DeSimone 2011) [12]. Subadult survival may respond most flexibly to changing environmental and population conditions (Gaillard et al. 1998; Eberhardt 2002). The importance of adult female survival again emphasizes that management

targeted at increasing or decreasing the survival of adult females should have the greatest influence on altering population growth downward or upward (see Logan and Sweanor 2010). In a Montana study, harvest-induced mortality doubled the importance of adult female survival to population growth while reducing the significance of kitten survival and maternity (Robinson and DeSimone 2011).

The Greater Yellowstone Northern Range cougar study population acted as a net contributor of cougars to surrounding areas both prior to and during wolf restoration. Yet the cougar population functioned as a “dependent source” because it relied on immigration for population growth (Hixon et al. 2002; Franklin et al. 2004; Newby et al. 2013). Given this, there appeared to be times when the contribution of emigrants from Yellowstone did indeed slow.

In the PW study the naturally restored and increasing population of cougars functioned similarly to those in areas where higher turnover of cougars as a result of hunting and depredation removals resulted in destabilized social structure, a younger age structure, and increased mortality of kittens by infanticide (Robinson and DeSimone 2011; Beausoleil et al. 2013; Wielgus et al. 2013). During this period the observed self-recruitment rate (0.98, table 16.3) was insufficient to maintain positive population growth without immigration from surrounding areas (Newby et al. 2013). Hence during population rebuilding, reliance on philopatry and immigration might suggest that the population was functioning as a population sink. Yet accounting for immigration

**TABLE 16.4.** Maternity rates, fecundity, and population growth estimates from six study areas in the western United States. The standard deviation is provided following the plus and minus symbol unless noted otherwise.

| Study                      | State               | Hunting Status              | $M_{x,adult,fem}$                   | Fecundity                         | Lambda ( $\lambda$ ) <sup>a</sup> |             | Observed                     |
|----------------------------|---------------------|-----------------------------|-------------------------------------|-----------------------------------|-----------------------------------|-------------|------------------------------|
|                            |                     |                             |                                     |                                   | Deterministic                     | Stochastic  |                              |
| Logan and Sweanor 2001     | New Mexico          | Reference area <sup>b</sup> | 1.4 ± 0.2 <sup>c</sup><br>1.3 ± 0.5 |                                   |                                   |             | 1.05 to 1.19                 |
| Logan and Sweanor 2001     | New Mexico          | Treatment area <sup>b</sup> | 1.6 ± 0.7 <sup>c</sup><br>2.0 ± 0.0 |                                   |                                   |             | 1.23 to 1.32                 |
| Lambert et al. 2006        | Washington          | Heavy                       | 1.27                                |                                   | 0.87 to 1.24 <sup>d</sup>         | 0.80 ± 0.11 |                              |
| Robinson et al. 2008       | Washington          | Heavy                       | 1.20                                | 0.45 ± 0.35                       | 0.89                              | 0.84 ± 0.21 | 1.00 ± 0.07                  |
| Cooley et al. 2009         | Washington          | Light                       | 1.12                                |                                   | 1.13                              | 1.10 ± 0.12 | 0.96 ± 0.15M<br>0.97 ± 0.26F |
| Robinson and DeSimone 2011 | Montana             | Heavy                       | 1.08                                | 0.42                              |                                   | 0.87 ± 0.08 |                              |
| Robinson and DeSimone 2011 | Montana             | Light                       | 1.40                                | 0.59                              |                                   | 1.01 ± 0.05 |                              |
| Pre-wolf study Murphy 1998 | Montana and Wyoming | Light to none               | 1.65 ± 0.43 <sup>e</sup>            | 0.70<br>(0.62, 0.72) <sup>f</sup> | See table 16.3                    |             |                              |
| During wolf study          | Montana and Wyoming | Light to none               | 1.07 ± 0.33 <sup>e</sup>            | 0.55<br>(0.50, 0.68) <sup>f</sup> | See table 16.3                    |             |                              |

<sup>a</sup> Rates of growth presented are from survival and fecundity life tables (deterministic and stochastic rates) and geometric growth ( $r$ ) from observed numbers of cougars each year where  $\lambda = \exp(r)$ .

<sup>b</sup> No cougars were removed from a reference area while 53 percent of adults were translocated from the treatment area over a 6.5-month period to simulate a onetime heavy harvest of cougars.

<sup>c</sup> Maternity rates are for periods of deer increase (top rate) and deer decrease (bottom rate) in the New Mexico study area.

<sup>d</sup> Growth rates started at 1.24 in 1998 and consistently declined to 0.59 in 2001–2 and 0.87 in 2002–3 as a result of declining female survival because of hunting.

<sup>e</sup> Maternity rates plus or minus the 95 percent confidence interval value.

<sup>f</sup> The 95 percent confidence intervals are given in parentheses.

and emigration revealed that the population remained a net contributor to the surrounding area. As the population filled in during the DW study, an older age structure and stable social relationships predominated. Declining growth was similar to declines observed in heavily hunted populations, where survival of adults and kittens was additive to other sources of mortality (table 16.4). Although growth slowed and declined toward the end of our study, the population contributed more emigrants to the surrounding area, particularly for female cougars, when compared to the PW period.

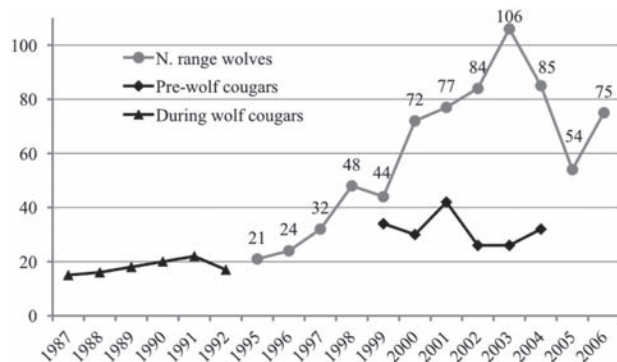
In conclusion, striving to set density targets for management in a given area will be misleading without accounting for immigration and emigration within the population structure and framework (Cooley et al. 2009; Newby et al. 2013) or for how competitor densities may alter habitat use for cougars. Without accounting for habitat use, the density of cougars viewed across the Greater Yellowstone Northern Range would appear to have changed little. But by assessing densities relative to habitat use, reproduction, and survival, we were able to tease out whether wolves affected cougars

by limiting their distribution, limiting their growth through reproduction and survival, or both.

## RATES OF INCREASE AND DENSITY OF COMPETITORS

Wolf populations have the potential for rapid increase, depending on causes of mortality and availability of prey (Mech and Boitani 2003a), and may at most times exceed growth rates achieved by cougars. The large Yellowstone elk population and initial high wolf pup production and survival, as well as the high survival of yearling wolves (86 percent) and adults (81 percent) through the years, resulted in rapid population growth—averaging 17 percent per year across all of Yellowstone but as high as 40 percent to 50 percent per year between 1995 and 2000 on the Northern Range (Smith and Bangs 2009). In the following years—2001 through 2004—growth slowed to 10–15 percent. On the Northern Range, peak numbers were also reached in 2003 at 106 wolves in seven packs (Smith et al. 2004b, 2005). As of December 2007, an estimated minimum of 1,513 wolves were present in





**FIGURE 16.4.** Total estimated number of cougars and wolves on the Greater Yellowstone Northern Range, 1987–2006. See tables 16.1 and 16.2 for cougar numbers and density estimates.

Montana, Idaho, and Wyoming (Sime et al. 2008). Since restoration in 1995, estimated annual wolf population growth rate has been greatest in the central Idaho recovery area ( $r = 0.293$ ,  $\lambda = 1.34$ ) and slightly lower in the Greater Yellowstone area ( $r = 0.224$ ,  $\lambda = 1.251$ ; Hamlin et al. 2009a). These rates, which precede management control by states, reflect growth when wolves received low mortality from humans.

Wolves, which largely depend on the same resources and which retained home ranges that were in similar size to those of female cougars, reached densities between 13 and 40 times greater than those of cougars (fig. 16.4). The highest density of wolves occurred on the Greater Yellowstone Northern Range because lower elevations provided suitable elk winter range and supported a large elk population. Thus about half the wolves lived on about 15 percent of the total area of Yellowstone National Park—present at densities of 44 to 106 wolves per 1,000 km<sup>2</sup> during our study (based on the ungulate winter range boundary; Smith and Bangs 2009). Following the end of our study, wolf numbers decreased substantially during the winters of 2006 and 2009 as a result of outbreaks of canine distemper virus associated with high mortality of pups (Almberg et al. 2009, 2010), intraspecific strife, food stress, and mange (Smith et al. 2011).

Estimates of grizzly bear numbers across the Greater Yellowstone area indicated that grizzly bears had tripled from 1987 to 2008, when numbers reached about 596 (Schwartz et al. 2010), yet their density in a given area may not exceed that of cougars. While black bear numbers remained largely unknown, the refined olfactory abilities of bears and their dependence on carrion in the system were reflected by

their ability to locate cougar kills and displace cougars at twice the rate wolves did. Hence the dominance hierarchy was not simply a function of numbers and growth rates but also a function of adaptations that enabled increased search efficiency, even at lower numbers. Given these adaptations, competitors with slower rates of growth or those occurring at lower densities may exceed those of more numerous competitors in the frequency with which they interact with subordinate species.

## SUMMARY

Cougar offspring dispersed over a relatively short time frame confined to summer in the PW study period, with 95 percent of offspring dispersing in June–August. During wolf restoration, cougar offspring initiated dispersal primarily during summer but dispersed over a longer time frame and into early winter: 92 percent of dispersals occurred in April, May, July, and September and 8 percent in October, November, and December. Contrary to our prediction that offspring should disperse earlier if resources became limited from competition with wolves and bears and there was little room to accommodate offspring, offspring instead reached independence and dispersed from their mothers at approximately five months older during wolf presence. Two explanations for this seemed plausible. A mother supporting young longer in a lesser-quality or riskier environment with few places for establishment would enable her young to grow larger and also more experienced with prey capture and in dealing with competitors. In addition to providing benefits to their offspring, mothers themselves might obtain group-related benefits from their association with large kittens, through increased vigilance in the group and because similar-size cougars may provide anti-predator benefits through intimidation.

Prior to wolves the naturally restoring population of cougars showed positive growth, with available territories near natal areas encouraging philopatry of females. Yet the observed self-recruitment rate was not sufficient to maintain positive population growth without immigration from surrounding areas. During population rebuilding, this reliance on philopatry and immigration might suggest that the population was functioning as a sink, yet accounting for immigration and emigration revealed that the population remained a net contributor to surrounding areas in the Greater Yellowstone Ecosystem. Following wolf restoration, an older



age structure and stable social relationships predominated. The philopatry of male offspring that we observed appears to be exceptional compared to other studies, but it perhaps resulted from the ability of dispersers to perceive information about conspecific density and habitat quality in both the natal area and surrounding patches they investigated during excursions. Adults did well at avoiding a growing wolf population, and offspring survived, but there was little room to accommodate philopatry or immigration of young cougars in the carnivore-rich environment. Few females stayed home, and the dispersal of young—particularly subadult females—increased from the PW period. Hence emigration of female offspring was at least partially density-dependent. Although growth slowed and declined near the end of our DW study, the population contributed emigrants more greatly to the surrounding area. Prior to and during wolf restoration, the Greater Yellowstone Northern Range

cougar population appeared to function as a “dependent source,” acting as a net contributor or source of recruits for surrounding areas but also relying on immigration in addition to philopatry for population growth. In the presence of the large Yellowstone elk population and absence of human mortality, the wolf population grew rapidly and reached densities between 13 and 40 times greater than the density of cougars on the Northern Range. Without accounting for changes in habitat use in the presence of wolves, the density of cougars viewed across the Northern Range appeared unchanged from PW estimates. However, because cougars strongly avoided wolves, their density almost doubled in habitats that provided refuge from competition. Striving to set density targets for management in a given area will be misleading without understanding population structure, assessing how competitors alter habitat use for cougars, or accounting for immigration and emigration.

### Text Box 16.1. Movements of Males

We first captured M127 on February 23, 1999, when he was approximately seven or eight months old and still with his mother. On November 1, 1999, at about fifteen to sixteen months of age, M127 left the study area and traveled ~55 km north outside Yellowstone National Park and into the Stillwater River drainage, Montana. He spent a little over one month roaming around near the Stillwater River before returning to his natal wintering area between Crevice Creek and Bear Creek on December 8, 1999. He remained in his winter natal area through winter 1999–2000, summer 2000, and winter 2000–2001. The area he used as an independent subadult overlapped resident adult male M137's territory by 85 percent. From predation sequences and GPS telemetry data, we documented that M127 was displaced from at least one of his kills by M137 and that they encountered each other on at least one other occasion. After one of these interactions, M127 became infected with FIV—we suspect from being bitten by male M137. Adult male cougar M137 killed three other independent subadult males during this time, but M127 survived and remained overlapped with M137. From January 5 through March 13, 2001, adult female F106—not male M127's mother—alternated spending time with both M137 and M127, later producing a litter of kittens we suspect were sired by M137. Female F106's behavior and vocalizations when consorting with M127 suggested that M127 was reproductively active (see text box 15.2). Adult M137 died of unknown causes—we suspected a heart problem or aneurism—on July 24, 2001. After this time M127 established a home range overlapping 35 percent of his natal area and became a resident

breeding male. Through his DNA we genetically linked M127 to siring three litters of kittens (not including the possible litter mentioned earlier), and he associated with two additional females (visually documented)—including his mother, F123—but he did not sire litters from these later associations. Instead, another resident male sired one of the litters, and F123 did not show denning behavior after spending time with her son. Male M127 was killed by wolves on November 21, 2004, when he was just shy of six-and-a-half years old.

Subadult male M170 and his sister, F158, were born to adult female F125 on February 19, 2002. Their father, verified through DNA and paternity exclusion analysis, was resident adult male M148. Male M170 became independent of his mother on April 21, 2003, but remained adjacent to and partly overlapped with his natal area. Although we did not acquire enough locations on him to calculate a home range, M170 remained within 3.6 km of the edge of his natal area and overlapped with a portion of his father's territory. Male M148 died on January 16, 2004, and M170 remained adjacent to his natal range at the end of our study during winter 2005–6. His radio collar dropped off on April 19, 2006, when he was four years and two months old, and we considered him an established resident adult around fall 2004. We documented one association between M170 and a female cougar around the time our study ended. Male M170, like longtime resident male M131, eventually moved north of the park boundary for unknown reasons, and M170 was treed by the same houndsman at the end of December 2007 and again at the end of January 2008.



## PART 5

### Carnivores and Humans

#### *Competition and Coexistence*

He who does not understand the uniqueness of individuals is unable to understand the workings of natural selection.

ERNST MAYR (1982: 47)

The story of Carnivores stretches back more than 40 million years and has involved the evolution of many strengths. The future of these magnificent animals is uncertain, but some aspects can be guessed at. The massive physical strength of a lion can drag a carcass it would take ten men to lift. But that strength cannot protect them, or the polar bears, or any other of these [carnivores], which now survive in reserves or areas beyond the reach of people. The cheetah, a monument to evolution's aimless engineer, can outpace any mammal since the beginning of time, but cannot evade the consequences of its genetic uniformity. Others display strength of character, in the versatility and quickness of wit with which the stone marten commandeers motor cars and red foxes survive, without degradation, the process of urbanization. As humans transform their world, these generalists can play by our rules and win. Above all else, the thrill of Carnivores lies in their individuality, each shaped by their ancestry, their ecology and their society.

DAVID MACDONALD (1992: 251)







## CHAPTER 17

### Synthesis

#### *The Niches of Cougars and Wolves*

In one sense, cougars and wolves occupy the same ecological niche (Elton 1927). The two species play similar roles in the community, as both are large predators that consume similar prey species within the Greater Yellowstone Northern Range. This Eltonian view of the niche is oriented more toward describing how an organism affects the environment—primarily by consuming resources in the case of cougars and wolves—than describing what environmental factors affect its existence (Leibold 1995). Following the return of wolves, at which time the spectrum of conditions and resources available for cougars became more limited, we found support for both interference and exploitation competition between subordinate cougars and dominant wolves and bears. This competition altered the niche-space of cougars from that before wolf presence (Hutchinson 1959; Caughley and Sinclair 1994; Begon et al. 1996). Therefore, in the absence of wolves and other dominant competitors, the niche of cougars probably expanded to include some areas that would be too risky to occupy in the presence of competitors. In the nearly seventy-year absence of wolves, elk, too, may have exploited areas previously too risky to occupy, perhaps enabling cougars to take further advantage of competitor-free conditions in Yellowstone (White et al. 2009c). If so, as cougars became restored across the West, their range may have increased from historical times when they lived in riskier environments. While competition structured the predator community, many species, including cougars and wolves, did eke out a living together.

In this chapter we summarize information from the preceding chapters with a focus on how wolf restoration and competition altered the boundaries of certain niche components of cougars. We also consider several factors that may moderate the outcome of competition between cougars and

wolves—such as dominance hierarchies, competition gradients, landscape heterogeneity, and individual behaviors (Keddy 2001).

## SUMMARY OF PERTINENT FINDINGS

### Competition for Food Resources:

#### Dietary Overlap and Loss of Food

Soon after the return of wolves, the diet of cougars and wolves overlapped substantially—with overlap indices ranging from 0.86 to 0.96—implying strong exploitation competition that had not yet led to divergence in resource use (fig. 17.1). During that time wolves and cougars competed with one another for available and vulnerable elk calves. As cougars and wolves shared the same food resources, wolves were better able to exploit patches of greater elk density. Subordinate cougars used forested and rugged terrain as refuge from competition with wolves, and they successfully foraged in lower-quality food patches.

As wolves became colonized and elk calves declined, the diets of cougars and wolves began to diverge, but only in the age and sex classes of elk each carnivore killed [1]. A decline in the abundance of elk calves equated to a trend of prey switching to adult cows by cougars and bulls by wolves. Yet both carnivores continued to prefer calves relative to their availability and so continued to compete with each other for this important source of food. As one food resource becomes more limiting, the diets of carnivores can eventually converge on alternate—often less abundant—prey as food becomes even scarcer (Wiens 1993; Sinclair et al. 1998; Kortello et al. 2007). Despite a 50 percent decrease in elk counts during the period 1995–2005, elk remained abundant at densities of 7–8 elk/km<sup>2</sup> (White and Garrott 2005). They also outnumbered mule deer by 4 to 1, suggesting that encounter rates with deer



**FIGURE 17.1.** *Bison are formidable prey for wolves, but when primary prey become a limited source of food, cougars might switch to deer and bighorn sheep that are using forested, rocky habitats, while wolves might perhaps focus more on bison and deer. Eventually, cougar and wolf diets should diverge more significantly. Photo by Dan Stahler, National Park Service.*

were likely substantially lower than encounter rates with elk for most cougars in our studies. In contrast to prey switching or apparent competition, the abundance of elk, coupled with winter migration of other ungulates, instead appeared to buffer the other ungulate prey from the impacts of cougar and wolf predation. We expected exploitation competition for prey to continue until elk became a limited resource, at which time cougar and wolf diets should have diverged more greatly—with cougars switching to deer and bighorn sheep that were using forested, rocky habitats and wolves perhaps focusing on bison and deer.

Although the frequency at which cougars killed prey did not increase substantially following the restoration of wolves, we found support for the prediction that frequent loss of food translates to increased rates of killing prey to compensate for those losses (table 17.1). Further, energy-maximizing and time-minimizing strategies as related to differing intraspecific and interspecific constraints affected handling time and move-

ment between kills in dissimilar ways. In contrast to predictions from energetic models, cougars and wolves killed prey at a higher rate than expected, and cougars killed at almost twice the rate of wolves when the biomass of prey and predator was considered. The rate at which cougars acquired prey during wolf restoration reflected the combined influence of killing large prey yet frequently losing carcasses to competitors. Feeding on kills for at times close to a week equated to greater chances of interference competition with large kills and of meat loss from freezing when temperatures plummeted.

In addition to the weight of killed prey, DW cougar kill rates increased 15–68 percent when a cougar was displaced from its kill by a wolf or a bear. Wolves visited one in four cougar kills and displaced cougars from at least one in thirteen kills, primarily during winter. Bears visited one in two cougar kills and displaced cougars from at least one in five kills—at almost twice the rate as they did prior to wolf restoration and at over twice the rate at which wolves displaced cougars.

**TABLE 17.1.** Summary of primary predictions and results from chapters 5, 6, 7, and 8. Text in ***bold italics*** indicates that our results supported this prediction.

| <i>Metric</i>                                                                            | <i>Prediction</i>                                                                                                                                                                                                                                                  | <i>Interpretation</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
|------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| CH. 5. PREY SELECTION                                                                    |                                                                                                                                                                                                                                                                    |                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| 1. Dietary overlap                                                                       | <b><i>High between cougars and wolves (greatest in early in DW period)</i></b><br>Low between cougars and wolves                                                                                                                                                   | Wolves select the same species and age classes of prey as cougars, supporting exploitation competition with cougars.<br>Cougars and wolves do not exploit similar types and age classes of prey, and exploitation of different prey enables subordinate cougars to coexist with wolves.                                                                                                                                                                                      |
| 2. Prey selection                                                                        | <b><i>No difference in prey species selection between PW and DW periods or between cougars and wolves</i></b><br><b><i>Greater proportion of elk calves in cougar diet</i></b><br>Greater proportion of nutritionally compromised or injured elk in wolf diet      | Given that elk remain abundant and are not a limited resource, cougars and wolves select similar prey types, and cougar selection of prey should be similar to prey selection prior to wolf presence.<br>Prey selection by cougars is limited by prey size, and prey selection by wolves is more strongly limited by condition.                                                                                                                                              |
| 3. Prey switching                                                                        | Divergence between late DW and PW periods ( <b><i>trend toward prey switching</i></b> )<br>Divergence between late DW cougar and wolves<br>Diets do not change ( <b><i>trend toward prey switching</i></b> )                                                       | Exploitation competition for prey leads to dietary shifts by subordinate cougars.<br>Prey are not yet limited such that competition strongly influences dietary shift by cougars.                                                                                                                                                                                                                                                                                            |
| 4. Habitat-hunting strategy                                                              |                                                                                                                                                                                                                                                                    |                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| a. Kills in forested, topographically complex areas, on greater slopes, and in less snow | DW cougar kills more so than PW cougars ( <b><i>supported for snow, not supported for forested/complex or greater slopes</i></b> )<br><b><i>DW cougar kills more so than wolf kills</i></b>                                                                        | In avoiding wolves, cougars kill prey in forested or topographically complex habitat with less snow more so than their PW counterparts because such areas enable catchability of prey and reduce risk of interference competition.<br>Cougars optimally stalk and kill prey in habitat that differs from that which facilitates the coursing hunting behavior of wolves, thus reducing interference competition between the two species.                                     |
| b. Prey use                                                                              | <b><i>DW cougar kills in lower prey use areas compared to wolves</i></b><br><b><i>DW cougar kills in lower prey use areas compared to PW cougars</i></b>                                                                                                           | In avoiding wolves, cougars kill prey in areas with lower prey use than their PW counterparts.<br>Wolves monopolize high prey use areas and cougars avoid wolves, thus reducing risk of encounter and interference competition at kills.                                                                                                                                                                                                                                     |
| CH. 6. KILL RATES                                                                        |                                                                                                                                                                                                                                                                    |                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| 1. Kill rates of cougars and wolves                                                      | Increased DW compared to PW, <b><i>trend toward increased maternal female rate</i></b><br>Decreased DW compared to PW with increased search time for prey<br><b><i>Greater frequency</i></b> and biomass killed per predator <b><i>for wolves than cougars</i></b> | Frequent competition at cougar kills results in displacement, and cougars must kill again more quickly.<br>Infrequent competition at cougar kills and/or searching for less abundant prey leads to longer search times and a lower kill rate for cougars.<br>Wolves are the dominant exploitative competitor for prey because of the energetic requirements of wolf packs, which equates to greater frequency of killing and higher kill rates compared to solitary cougars. |
| 2. Seasonal kill rates                                                                   | Increased DW winter compared to PW winter<br><br>Lower in winter                                                                                                                                                                                                   | Greater overlap with wolves during winter months results in increased interference competition for cougar kills during winter.<br>Cougar winter kill rates increase as a result of predation facilitation by wolves.<br>Cougars show a functional response to the increased density of ungulates young during spring birth resulting in a higher frequency of killing during spring-summer.                                                                                  |

*continued on next page*



TABLE 17.1—continued

| <i>Metric</i>                        | <i>Prediction</i>                                                                                                                                             | <i>Interpretation</i>                                                                                                                                                                                                                                                                                                                                                                                                                                             |
|--------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 3. Factors that influence kill rates | <b>Greater influence of displacements, prey weight, and winter DW compared to PW</b><br><br>Positive with wolf population and wolf use                        | Variation in kill rates is influenced by competitor use of the landscape, availability of elk calves, seasonal differences, and the frequency of interference competition at kills.                                                                                                                                                                                                                                                                               |
| CH. 7. INTERACTIONS AT KILLS         |                                                                                                                                                               |                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| 1. Frequency of displacement         | <b>Greater DW compared to PW</b>                                                                                                                              | Interference competition increases with a greater density and encounter rate with large competitors.                                                                                                                                                                                                                                                                                                                                                              |
| 2. Odds of displacement by wolves    | <b>Greater for large ungulate prey kills</b> , in open cover types, on gradual slopes, <b>with higher wolf use, during winter</b>                             | Prey size, landscape features, season, and intensity of wolf use influence wolf displacement of cougars from their kills.                                                                                                                                                                                                                                                                                                                                         |
| 3. Odds of displacement by bears     | <b>Greater for large ungulate prey kills, during spring</b><br><b>Decreases with increasing availability of carcasses</b>                                     | Prey size, landscape features, season, and availability of carcasses influence bear displacement of cougars from their kills.<br>Alternatively, certain landscape features enhance concealment of kills by cougars, reducing interference competition.                                                                                                                                                                                                            |
| CH. 8. COMBINED INFLUENCES           |                                                                                                                                                               |                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| Total predation rate                 | <b>Increased DW compared to PW, greatest for elk calves</b><br><br><b>Inversely density-dependent; compensatory when added to wolves</b>                      | Exploitation competition for prey reduces the number of prey available and interference competition for dead prey increases predation rates by cougars, resulting in increased offtake of elk, adding to offtake by wolves, bears, and humans.                                                                                                                                                                                                                    |
| Elk population growth                | <b>Greater limitation DW than PW, becoming additive to other sources of mortality</b><br><br>Lower limitation DW than PW, not an additive source of mortality | An increasing ratio of carnivores to elk, increased competition for and offtake of elk calves by carnivores, and sustained hunter harvest of prime-age cow elk are additive top-down forces strongly limiting growth of the elk population.<br><br>The cougar population is strongly limited by competition with wolves and bears and prey become so limited that the cougar population declines significantly, thus reducing cougar predatory influences on elk. |

Large prey tended to be killed by cougars on less steep slopes in open areas, which were areas with greater wolf use and also areas of enhanced detection of carcasses by bears. The longer time spent feeding at large kills than at small kills, combined with their greater visibility to scavengers, translated to even greater risks of displacement for cougars. Cougars lost as little as 0.94 kg/day of ungulate biomass for small ungulate prey to as much as 28 kg/day for large ungulate prey—or 20 percent to 100 percent of their daily energy requirements—when they were displaced from kills.

While interference competition from bears at kills was double that of wolves, selective pressure to avoid bears may not be as great as that associated with risk of death from wolves. Bears appeared focused on securing the meal, whereas wolves sometimes chased and treed cougars without returning to the kill to feed. Despite the fact that their kills were frequently detected in the complex habitat of the Greater Yellowstone Northern Range, concealment of

kills—dragging carcasses to dense vegetation and covering them with debris—remained an adaptive behavior for this solitary felid in minimizing detection and loss of carcasses to competitors. Even in areas used frequently by wolves and bears, terrain features such as steep slopes and rough topography may hinder wolf or bear discovery of cougar kills and enable kills to remain undetected.

### Landscape Use: Spatial-Habitat Overlap

We found differences in cougar home range structure, habitat use, and population density mostly consistent with what we expected, given that wolves were the dominant competitor (table 17.2). After wolf restoration, female cougars maintained home range sizes similar to those of PW females but shared a modestly greater portion of their home range and core area with a greater number of other DW females. Male cougars maintained comparable territorial overlap with other DW male territories in spite of having smaller home



**TABLE 17.2.** Summary of primary predictions and results from chapters 10 and 11. Text in ***bold italics*** indicates that our results supported this prediction.

| <i>Metric</i>                           | <i>Prediction</i>                                                                                                  | <i>Interpretation</i>                                                                                                                                                                                                                                                                                                          |
|-----------------------------------------|--------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| CH. 10, HOME RANGES AND MOVEMENTS       |                                                                                                                    |                                                                                                                                                                                                                                                                                                                                |
| 1. Home range size                      | <b><i>Smaller DW (for males only) than PW</i></b><br>Larger DW than PW                                             | Avoidance of wolves results in retraction of home range sizes.<br>Cougars incorporate disjunct areas of hunting and security habitat.                                                                                                                                                                                          |
| 2. Home range fidelity                  | Lower DW than PW<br><br>Greater for females than males                                                             | PW cougars exhibit stable social structure; DW cougars shift home ranges, as wolf territories and prey are spatially and temporally less predictable from year to year.<br>Familiarity with prey and escape resources in an area should enhance the survival of offspring.                                                     |
| 3. Cougar-cougar overlap                | <b><i>Greater DW</i></b> than PW<br>Greater for females than males                                                 | In avoiding wolves, cougars use optimal habitat more than PW cougars.<br>Males defend their territories, and females are more likely to share resources.                                                                                                                                                                       |
| 4. Cougar-wolf overlap                  | <b><i>Lower for core areas than total home range</i></b><br><br>Greater overlap with wolves during winter.         | Cougar core areas are situated away from or in between core areas of wolf territories, enabling cougars to avoid encounters with wolves in areas used most intensively.<br>Cougars are less able to segregate themselves spatially from wolves when congregated with prey on winter ranges.                                    |
| 5. Cougar-wolf activity patterns        | Cougars active at different times than wolves                                                                      | Cougars avoid wolves by hunting at times when prey are less active.                                                                                                                                                                                                                                                            |
| 6. Cougar core-periphery movement       | <b><i>Accelerated movement rates in periphery (for females only) compared to core area</i></b>                     | Periphery areas overlap with wolf home ranges and are a riskier, less secure part of a cougar's home range.                                                                                                                                                                                                                    |
| CH. 11. SPATIAL-HABITAT USE             |                                                                                                                    |                                                                                                                                                                                                                                                                                                                                |
| 1. Cougar use of wolf areas             | <b><i>Avoid high wolf use areas</i></b>                                                                            | Cougars reduce competition and the potential for direct encounters by using habitats containing low density of wolves.                                                                                                                                                                                                         |
| 2. Cougar avoidance of wolves           | <b><i>Greater in winter</i></b><br><br>Lower in winter                                                             | Avoiding encounters with wolves is paramount during winter when wolf pack cohesion and overlap with cougars is greater than during summer.<br>Condensed winter range does not allow for avoidance of wolves, while less overlap during summer allows for greater avoidance.                                                    |
| 3. Cougar use of escape terrain         | <b><i>Greater DW than PW</i></b><br><br><b><i>Greater for female cougars</i></b><br><b><i>Lower for wolves</i></b> | Cougars avoid wolves by seeking steep, rocky terrain that inhibits travel and pursuit by wolves.<br>Protection of kittens from wolf encounters.<br>Cougars are better exploiters of rugged terrain while wolves exploit open terrain, reflecting the different hunting, territorial, and escape strategies of the two species. |
| 4. Cougar use of prey-rich areas        | <b><i>Cougars in areas of lower prey density than wolves</i></b>                                                   | Wolves competitively exclude cougars from high prey density areas.                                                                                                                                                                                                                                                             |
| 5. Cougar density on the Northern Range | Lower DW<br><br><b><i>Higher DW</i></b>                                                                            | Cougar population approaching carry capacity and new individuals occupying more marginal habitat at the periphery of the most suitable areas.<br>Wolf use constrains cougars to the most secure habitat.                                                                                                                       |

ranges that overlapped more females compared to PW males. Cougar home ranges and core areas overlapped considerably—58 percent to 98 percent—with multiple wolf packs. Despite cougars sharing substantial portions of their home

ranges, cougars used core areas situated away from the areas used most intensely by wolves.

Cougars maintained similar habitat selection across both study phases but increased their use of forested and rough

terrain after wolf restoration. In winter cougars clearly avoided wolves—males more so than females. The onset of summer relaxed the constraint of wolves to some degree, although cougars still avoided areas used most heavily by wolves. Habitats that provided greater security for cougars were little used by wolves, which preferred more open terrain. Cats traded off opportunities to hunt in areas used most heavily by elk. Also as we predicted, cougar home ranges during wolf restoration encompassed areas of lower elk use compared to cougar home ranges prior to wolf restoration. These differences were most noticeable in the core area of cougar ranges, yet core areas were where cougars made most of their kills. Subordinate cougars may survive best in refuges from competition with low prey abundance because areas rich in prey are dominated by larger, more aggressive wolves.

Female cougars took greater risks and ventured farther from escape cover within their core summer home ranges. Yet they remained closer to cover when in the periphery of their home range, which overlapped with wolf territories more than did their core areas. As wolves were restored on the Greater Yellowstone Northern Range, cougar population density increased because of both a modest increase in population size and a decrease in total area used, resulting from cougars' more intensive use and sharing of the most secure habitats. Competition refuges that enable partitioning of habitat and landscape features may reduce the need for competitors to partition other resources, such as food, as long as prey do not become limiting. In other words, cougars and wolves may have exploited similar prey with little dietary differentiation because prey were not a limited resource, and the intermix of rugged terrain and open grasslands on the Northern Range provided ample opportunity for habitat partitioning between cougars and wolves.

### **Population Performance: Limiting Effects of Wolves?**

Exploitation competition for food and habitat, as we documented between cougars and wolves, may contribute to limiting the production and population growth of one competitor, most commonly the subordinate competitor. Yet many of our predictions of competition reducing population performance were not supported, which perhaps resulted because cougars quickly adjusted to wolves and used competition refuges and because prey were not a limited resource

(table 17.3). Further, the differences we did find between the PW and DW periods were also influenced by the increasing population and changing social structure of cougars prior to the arrival of wolves. We found support for the prediction that frequent loss of food translated to increased rates of killing prey, but the lower maternity rates of females during wolf restoration than prior to wolves were most strongly influenced by the time between subsequent births, as there was lack of variation in litter size and in reproductive activity by age. The number of DW females producing litters each year was linked to females supporting their offspring for longer periods in a riskier environment; hence a longer interval between successive births.

Within the time frame of our study, exploitation and interference competition did not reduce cougar survival, but causes of mortality as a result of interspecific interactions replaced those that resulted from intraspecific interactions. Survival rates of independent adult females and males remained high as wolf numbers increased, but survival rates differed for kittens. The survival of kittens improved instead of declining following the return of wolves. The improved survival of kittens during wolf restoration and declining prey abundance probably resulted from mothers supporting and providing safety to their offspring for longer periods of time. During wolf presence, kittens reached independence from their mothers and dispersed from the study area at approximately five months older than prior to wolf presence. An older age structure of DW cougars and stable social relationships predominated. As we have noted, cougars could defend and provision offspring more effectively in a context of naturally low turnover and stable social relationships. And mothers themselves might also have obtained group-related benefits from their association with large kittens because similar-size cougars may provide anti-predator benefits through intimidation and through increased vigilance in the group.

In the presence of the large Yellowstone elk population and absence of human-caused mortality, the wolf population grew rapidly and reached densities from 13 to 40 times greater than the density of cougars on the Northern Range. Without accounting for changes in habitat use in the presence of wolves, the density of cougars viewed across the Greater Yellowstone Northern Range appeared unchanged from PW estimates. However, because cougars strongly avoided wolves, their density almost doubled in habitats

**TABLE 17.3.** Summary of primary predictions and results from chapters 14, 15, and 16. Text in ***bold italics*** indicates that our results supported this prediction.

| <i>Metric</i>                                   | <i>Prediction</i>                                                                                                                                                                                                           | <i>Interpretation</i>                                                                                                                                                                                                                                                                                                                                       |
|-------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <b>CH. 14 AND 15: REPRODUCTION AND SURVIVAL</b> |                                                                                                                                                                                                                             |                                                                                                                                                                                                                                                                                                                                                             |
| 1. Age structure, breeding and birth patterns   | Younger age structure in DW compared to PW<br>Broader distribution to breeding and births in DW compared to PW                                                                                                              | Exploitative and interference competition with wolves leads to shifting spatial structure, increased instability, and hence younger age structure of cougars and changes in timing of breeding and birth of young.                                                                                                                                          |
| 2. Productivity and maternity rates             | Smaller litter size in DW compared to PW<br><b><i>Lower maternity rates in DW compared to PW</i></b>                                                                                                                        | Frequent displacement from kills and/or searching for less abundant prey leads to increased energy demands on females, reducing productivity.                                                                                                                                                                                                               |
| 3. Causes of mortality                          | <b><i>Increased interspecific killing in DW study compared to PW study</i></b>                                                                                                                                              | Greater overlap with more competitors results in an increase of interspecific killing during direct interactions.                                                                                                                                                                                                                                           |
| 3. Survival rates                               | Lower in DW compared to PW, particularly for maternal females, dependent kittens, and subadults<br><br>Lower in winter in DW compared to PW<br><b><i>Decreases with increasing wolf use, hunting season outside YNP</i></b> | A growing number and density of dominant competitors results in increased competition and reduced survival of subordinate cougars, with kittens and subadults most vulnerable.                                                                                                                                                                              |
| <b>CH. 16: DISPERSAL AND POPULATION CHANGE</b>  |                                                                                                                                                                                                                             |                                                                                                                                                                                                                                                                                                                                                             |
| 1. Independence and dispersal                   | Younger average age in DW compared to PW                                                                                                                                                                                    | If resources became limited from competition and there was little room to accommodate offspring, ending maternal care of offspring earlier should enable an adult female to devote her energy to obtaining resources for raising a new litter.                                                                                                              |
| 2. Emigration                                   | Reduced in DW compared to PW<br><br><b><i>Similar or increased in DW compared to PW (supported for females)</i></b>                                                                                                         | Exploitation competition for prey and space and mortalities from direct interactions result in fewer cougar progeny produced and surviving and reduced emigration rates of offspring.<br><br>Offspring that do survive emigrate at a greater rate, resulting from increased exploitation competition for prey and space, and fewer females are philopatric. |
| 3. Population growth                            | <b><i>Increasing in PW and decreasing in DW (partly supported)</i></b>                                                                                                                                                      | Lower reproductive rates and survival rates translate to lower population growth and population limitation by dominant competitors.                                                                                                                                                                                                                         |

that provided refuge from competition. Prior to the restoration of wolves, the population of cougars showed positive growth, with available territories near natal areas encouraging philopatry of young female cougars. Following wolf restoration, adult cougars did well at avoiding the growing wolf population and offspring survived, but there was little room to accommodate philopatry or immigration of young cougars in the carnivore-rich environment; population growth slowed, and then populations declined in the later years of the DW study. In addition, after wolf establishment abundance of prey was not yet limiting, as there was no indication of increased aggression between cougars or of starvation. Yet areas that provided refuge from competitors may have been limiting as cougars overlapped highly in habitat, providing advantages to them over wolves.

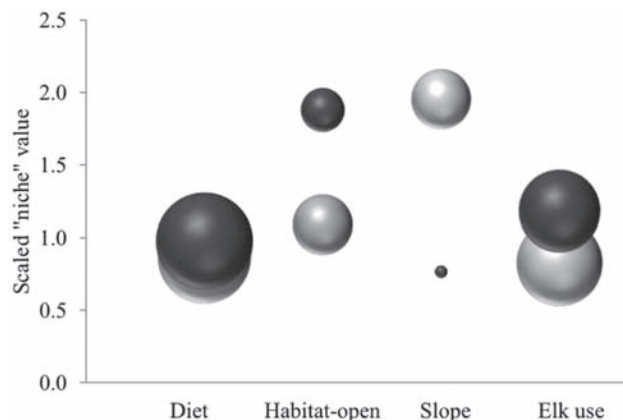
## CONCLUDING THOUGHTS: COMPETITION AND NICHE PARTITIONING

Wolves can have at least locally strong effects on the ecology of cougars (see also Kortello et al. 2007). By virtue of wolves being a dominant interference competitor, wolf populations are likely to suffer little niche contraction in the presence of subordinate competitors, while the converse is true for cougars. Still, local coexistence and the niches of both cougars and wolves should be dynamic, changing with different densities of each carnivore and as habitat and prey change with diversity and productivity of the environment. Unlike other studies where the density of subordinate carnivores was limited by dominant competitors, competition with wolves had not limited the number of cougars over the course of our study (Gorman et al. 1998; Creel 2001). Instead, habitats

with complex structure habitats provided refuge and enabled cougars to persist at elevated densities within a smaller area of prime habitat while our study was under way. The competitive balance also hinges on the evolutionary history and adaptations of each species, body size and dominance, individual behaviors, and the management imposed by humans within and across environmental gradients (Johnson et al. 1996; Durant 1998; Creel and Creel 2002).

### Competition Gradients and Landscape Heterogeneity

Gradients in timing and intensity of competition occur in nature (Caughley and Sinclair 1994; Keddy 2001), with cougars and wolves competing more intensely along one niche dimension and less so along another. Perhaps unique compared to other areas of the western United States, the Greater Yellowstone Northern Range is characterized by a diverse and abundant assemblage of ungulates and a heterogeneous landscape that supports a diverse array of carnivores, similar to carnivores co-occurring in heterogeneous environments across portions of Africa (Johnson et al. 1996: 206; Durant 1998; Creel and Creel 2002). Such diverse landscape characteristics may de-couple interactions between competitors and enable as well as stabilize their coexistence (Denno et al. 2005). As an example, figure 17.2 shows interspecific overlap between cougars and wolves along four niche dimensions related to winter diet and habitat components of winter kill sites. Although we documented high exploitation competition for prey between cougars and wolves, cougars first made adjustments not in diet but in finding safe sites to forage, mate, and rear offspring. There was also greater separation in where they killed prey, with cougars killing prey in or near forested, rugged terrain and on higher slopes than wolves. Cougars gained refuge from wolves and bears, which were either physically excluded from accessing complex structured habitats or which had their foraging behavior impaired in those habitats (Denno et al. 2005). The niches of wolves and cougars most strongly diverged in habitats that enabled each species to be a superior exploitation competitor in its own right. While wolves are well adapted to open terrain, other habitats remained more permeable to them compared to cougars' ability to exploit open terrain. Wolves traveled through all but the most rugged places of the Northern Range, while cougars rarely (<4 percent of locations; chapter 11) ventured beyond 100 meters from cover.



**FIGURE 17.2.** Interspecific overlap between cougars (gray bubbles) and wolves (black bubbles) along four niche dimensions during winter as an example of gradation of exploitation competition enabling coexistence along certain niche dimensions. The four niche components represent a mixture of categorical data (diet) and continuous data scaled for representation, with the size of bubble representing the scaled 95 percent confidence interval associated with the scaled metric.

Adaptations that evolved long ago as cougars and wolves competed for food and space were apparent during our study. Cougar mortality from direct interactions with wolves occurred infrequently, perhaps resulting from the process of natural selection, which selected for and maintained cougar behaviors that enabled them to balance maximizing foraging opportunities, access to mates, and protection of young while minimizing risk of encounter with competitors. Even in the long absence of wolves, cougars maintained behaviors that placed them in and near habitats that provided escape. Bears, too, likely helped shape the adaptive traits we see in present-day cougars. By being adapted to exploit forested, rugged terrain, cougars were able to use low-density prey and better able to conceal kills from competitors. Cougars are less vocal than other carnivores, with the loudest vocalizations occurring during mating, and these vocalizations may be buffered from traveling far by the forested and rough terrain in which they occur. These habitat preferences and the mosaic of habitat on the Northern Range enabled cougars to mitigate competition risk and seek refuge from competitors and no doubt helped cougars survive in a landscape where wolves and bears dominate. In this manner, the availability of refuges from competition might most strongly govern the ability of cougars and wolves to partition their niches along certain dimensions.



### Individual Traits and Competitive Performance

Coupled with landscape structure, a gradient in how wolves used the landscape was apparent across the Northern Range, resulting in risk that was not equal for all cougars at all times. For instance, some cougars experienced relaxed risk of competition from wolves in spring and early summer, when wolves were busy with denning and rearing pups and when movements were localized around rendezvous sites at lower elevations and on lower slopes. Wolves also foraged less cohesively during summer (Metz et al. 2011); hence a cougar that encountered fewer wolves or single wolves should have had an increased chance of escape or of dominating any direct interaction. In contrast to summer, wolves foraged more cohesively during winter but also had a more aggregated distribution. Consequently, a cougar that moved away from wolves once they were seen or heard might have had a better than average chance of moving into an area with lower densities of competitors (Colegrave 1997; Durant 2000). When the risk of altercation increased during winter, cougars significantly reduced their use of high-risk habitats. Many of these temporally and spatially adaptive movements occurred at finer scales than the data we collected, and studies that further elucidate tradeoffs between foraging risks and energetic costs may prove beneficial to managing cougars in competitive environments.

Cougars may also gain positive fitness benefits if competitor density provides information about resources (Forsman et al. 2002; Fletcher 2007; Forsman 2008). During summer most females selected for intermediate ranges of wolf use while using lower and higher wolf use areas less (see figs. 13.9c, 13.10b). For some individuals, lower to intermediate densities of wolves may provide an optimal solution to the tradeoff between poor habitat and competition. Unlike females, male cougars did not express selection for a mid-range of wolf use and instead exhibited a monotonic increase with increasing wolf use. We suspect that this occurred because male home ranges were already situated in highly secure areas, and unlike females supporting offspring, males may not have had to make tradeoffs between hunting and wolf avoidance. Clearly, there are overall patterns in how cougars partitioned the landscape, but gender and individual nuances were also apparent.

Such differences among individuals or individual variation within a population are important to understand not only the evolution of life histories but also the resiliency and

persistence of populations (Holmes and Sherry 1997; Horne 1998). The individual behaviors and abilities of cougars, as illustrated by females F125 and F107 in text boxes 17.1 and 17.2, relate to how cougars are managed when living in competitive environments (see chapter 18). When we simulated loss of these two females in various years of the study, maternity rate declined by 13–20 percent and fecundity by 15–27 percent. When we similarly removed two other adult females we monitored for the longest periods of time, F47 and F106, maternity rate declined by an average of 7 percent and fecundity by an average of 5 percent. In particular, female F125 contributed large, experienced offspring to areas beyond Yellowstone's boundaries.

### DOMINANCE AND THE SHIFTING BALANCE OF INTERFERENCE AND EXPLOITATION COMPETITION

Similar in size, cougars and wolves might coexist in fluctuating environments if their competitive abilities were equivalent and symmetric (Keddy 2001). A scaling of comparison based on ratio of biomass (mass of prey:mass of predator) revealed that when wolves killed cougars, the biomass of wolves outweighed cougars by almost 13 times. In the two instances when solitary wolves were killed by a cougar, the biomass ratio of cougar to wolf averaged 1.0:1.0 (range = 1.0:0.9 to 1.0:1.1). The strong discrepancy in dominance meant that cougars were generally poor interference competitors—ineffective at defending food, young, or themselves during direct encounters. Flight into secure habitat or, better yet, avoiding competitors when possible presents an enhanced strategy for survival. When one-on-one interactions do occur, a cougar might have advantages over a solitary wolf because of similar body weight, ability to ambush, and ability to manipulate and kill prey quickly. Cougars have proven successful at killing solitary wolves, typically young dispersers, during encounters at cougar kills (Jimenez et al. 2008; Ruth 2004c).

Although decreasing similarity in competitive ability or size leads to dominance, subordinate cougars could still remain superior at exploiting certain conditions, even if they were poor interference competitors (Polis et al. 1989; Holt and Polis 1997; Linnell and Strand 2000). Cougars and wolves exhibit high levels of dietary overlap, ranging from 44 percent to 91 percent in northern systems, with the lower percentage occurring after cougars switched their diet to alterna-

tive ungulate prey (Renkonen index of overlap, Ruth 2004a; Kortello 2005). These studies and the high dietary overlap of Greater Yellowstone cougars and wolves (82 percent across seasons) reveal strong exploitation competition for relatively abundant prey (Renkonen index, Murphy and Ruth 2010), with wolves better exploiters of large, adult elk and cougars better exploiters of elk calves. The ability of cougars to exploit a greater diversity of prey—such as bighorn sheep, pronghorn, and occasionally mountain goats—suggests that cougars should be better exploitative competitors when access to primary prey is limited. When we consider only ungulate prey, Greater Yellowstone cougars had a standardized niche breadth seven times that of wolves [2]. Plasticity in diet might be especially important for females, as we noted that adult and maternal females killed a greater diversity of ungulate prey than did male cougars.

While much of our focus was on the influence of wolf restoration on cougar ecology and behavior, bear numbers also increased, and through displacement, bears had a stronger influence on the kill rate of cougars than did wolves. Yet they appeared less of a direct threat to the survival of the individual cougars they displaced. In the end, bears focused on the meal to be had, while wolves posed greater risk of injury or death to cougars.

Competition over dead prey brings into question whether high prey density weakens competition, as standard competition theory predicts, or whether it may increase competition by supporting greater densities of competitors that interact more commonly over more abundant carcasses (Creel et al. 2001). The answer to this question may differ for different ecosystems and competitive environments. On the Greater Yellowstone Northern Range, high prey density supporting high densities of carnivores did seem to weaken competition for cougar-killed prey. The greater presence of carcasses reduced competition for cougar-killed prey, as bears focused on other carcasses and wolves potentially scavenged less frequently because of high encounter rates with prey. While this occurred for subordinate cougars, bears may have competed more strongly with wolves for wolf-killed prey. Competition for cougar-killed prey increased as prey density declined,

particularly as elk calves became less abundant and cougars killed an increasing proportion of larger prey. Strong interference competition at kills might eventually reduce cougar densities, which should also weaken exploitation competition for prey and space.

At high prey densities supporting high densities of carnivores, competition for space did increase, with cougars seeking out habitats that provided refuge and thereby reduced direct encounters with wolves. On the one hand, shifts in spatial-habitat use by cougars probably reduced chances for interference competition with wolves and weakened exploitation competition for habitat. On the other hand, seeking refuge from wolves did not weaken exploitation competition for prey while prey declined yet remained relatively abundant. If the types and abundance of food became more limited, which appeared to be occurring following the end of our study, exploitation competition for food and habitat perhaps intensified. If so, subordinate cougars then might take greater risks to acquire limited prey, including increased use of less preferred habitat within home ranges and perhaps reduced home range fidelity or shifts into areas that offer more marginal habitat or food (Koehler and Hornocker 1991; Litvaitis 1992; Johnson et al. 1996; Durant 1998). We wondered about this latter possibility, as at the end of our study one long-established resident male and one newly established male apparently abandoned their territories when they moved north outside the park boundary.

Relegated to higher-elevation, timbered habitats, the niches of both cougars and wolves are further constrained by competition with humans. Better able to exploit the once broad open valleys and grasslands that humans have preferred for development, wolves might now overlap cougars more than they did historically (Riley et al. 2004). Our study was conducted in a relatively pristine setting with fewer human influences than in other areas. How human influences, differing landscape characteristics, and site-specific effects of ungulate management may contribute to or moderate interactions of cougars and wolves is an area ripe for further study.

**Text Box 17.1. Meet F125**

Female F125, known to us as Savannah because she was not bashful about using more open terrain, was first captured in March 2001, when she was about 4.5 years old (fig. 17.3). As we radio-tracked her, we documented 93 of her kills. Her home range was completely subsumed by the cumulative territories of wolf packs, and she primarily contended with the Leopold, Rose, Rose2, and Geode wolf packs. The area she used most intensively, her core area, was wedged between the core areas of wolf packs. Yet she frequently contended with wolves and bears stealing her kills. She was displaced from 37 percent of these kills—8 percent by wolves and 29 percent by bears. Overall, 75 percent of her kills were detected by other carnivores, with an unknown number of displacements possibly occurring. This should have been

extremely costly for her, and indeed her kill rate increased after displacements by wolves or bears. However, we found her to be a highly successful mother, and she expressed what we viewed as confidence in dealing with a risky environment. Her skill at killing a wide variety of prey was reflected in her dietary breadth—she successfully killed adult elk, pronghorn, bighorn sheep, mule deer, and white-tailed deer. During the time we followed her, she produced four litters consisting of nine offspring. One of her kittens died as a result of wolf predation, but the other two kittens in that litter survived. She successfully raised 67 percent of her kittens to independence and dispersal from the study area. Female F125 was about 10 years old at the end of our study, and the fate of her two kittens at that time is unknown.



**FIGURE 17.3.** Female F125 after her first feeding on an elk. We found F125 to be a very successful mother and skilled hunter, and she expressed what we viewed as “confidence” in dealing with a risky environment. Photo by Dan Stahler, National Park Service.



**Text Box 17.2. Meet F107**

We first captured F107 as a 3.5-year-old adult in February 1999 and followed her for slightly longer than female F125 (fig. 17.4). During the years 1999 through 2003, F107 spent her summers overlapping Soda Butte and Pebble Creek and the surrounding peaks: Abiathar, Baronette, and Mount Norris. Her home range (95 percent fixed kernel) overlapped combined wolf territories by 80 percent to 96 percent, but she mostly had to contend with the Druid and Rose2 wolf packs early on and later the Geode and Druid wolf packs. As we followed her movements, we documented 26 of her kills. She was displaced from 12 percent of these kills—8 percent by wolves and 4 percent by bears. Yet 50 percent of her kills were detected and possibly scavenged by other carnivores, and she may have been displaced in some of these instances.

Like female F125, female F107 was quite consistent at producing litters of kittens. During the nearly seven years we followed her, she produced 5 litters consisting of 15 offspring. Of those offspring, 60 percent (9 kittens) died before they reached an age to disperse from the study area. Four kittens in one litter were killed by wolves, and 3 starved to death as she moved them from summer to winter range. Of the kittens that did survive, 4, or 27 percent, survived to disperse from the study area, while 2 had unknown fates at the end of our study. Although, like female F125, F107's maternity rate was high, her reproductive success was low and heavily influenced by wolves, winter conditions, and poor access to prey as fall transitioned to winter. Her strategy to shift to a new summer territory may have benefited her survival and reproduction. Female F107 was over 10.5 years old at the end of our study and had produced a litter of kittens, but we do not know the fate of this litter.



**FIGURE 17.4.** Female F107, like female F125, was a consistent producer of offspring, but she struggled to raise her young to independence and dispersal, losing one entire litter of four to wolves in 1999. Photo by Dan Stahler, National Park Service.



## CHAPTER 18

### Management and Conservation of Cougars *Considering Interspecific Competition*

All organisms compete at some level for space to live and resources that enable survival and reproduction, thus influencing the balance of coexistence. The biological niche of large carnivores at the top of the food chain and their low reproductive rates mean that they will always be less abundant than their herbivore prey (Macdonald 1992; Sillero-Zubiri and Laurenson 2001). The larger the carnivore, the more food and space it needs and the rarer it is likely to be, thus posing challenges for coexisting in a human-dominated world. Elsewhere in the world, large carnivores and other wildlife are declining under the pressure of habitat degradation, hunting, conflicts with humans and their livestock, disease, and the commercial trade in body parts (Weber and Rabinowitz 1996). Thirty-five species of wild cats are not faring well or we simply know too little about them. Given these statistics, cougars are an icon of North America—our only large cat, which has shown undeniable resiliency in living in competitive environments (Hornocker and Negri 2009).

Over the course of this book we have illuminated the fact that interactions between large carnivores—via exploitation and interference competition—play a substantial, often complex role in the dynamics of cougar predation, movements, and habitat use. Because large carnivores exert direct and indirect effects, their presence leads to myriad effects on other species and processes that make ecological systems healthier and more resilient (Bowyer et al. 2005; Ray et al. 2005; Estes et al. 2011; White et al. 2013). For instance, cougars and wolves have influences both up and down the food chain by providing food to larger competitors and scavengers and through intraguild predation on smaller carnivores such as coyotes and foxes. Considering the ecological frame-

work in which large carnivores operate carries broader implications for the maintenance of biodiversity (Ray et al. 2005; Estes et al. 2011; White et al. 2013).

Conservation and management of wildlife are all about an attempt to reconcile the needs and requirements of wildlife with the desires, needs, and expectations of human beings (Mech and Boitani 2003a; Hornocker and Negri 2009). Although interspecific interactions are increasingly recognized as widespread within guilds of carnivores, their importance is often underappreciated in management, as efforts have most typically focused on a single carnivore species and its relationship to prey (Palomares and Caro 1999; Linnell and Strand 2000). Information on large carnivores has advanced over the past thirty to forty years, and much of this information has been distilled into specific management and conservation recommendations within states and across regions. We direct readers to these substantial works for valuable information relative to cougars, wolves, bears, and other large carnivores (Logan and Sweanor 2001; Mech and Boitani 2003; Clark et al. 2005; Ray et al. 2005; Hornocker and Negri 2009; Jenks 2011; White et al. 2013). The take-home message from almost all of these publications is that three overriding ecological stressors—acting at larger scales than the boundary of protected areas like Yellowstone—cannot be ignored if large carnivores are to remain as part of functioning ecosystem processes. They are: (1) habitat loss and fragmentation; (2) direct killing by humans, including poaching; and (3) climate change.

Our goal in this final chapter is to highlight some topics we see as important to integrating concepts of competition and other aspects of cougar biology within the framework of management and conservation of large carnivores. Involving

the public as stakeholders in management and conservation planning within local landscapes has been—and will continue to be—essential.

### COMPETITION FOR SPACE AND PREY: CARNIVORES AND HUMANS

- *Coexistence with large competitors may reduce available habitat for cougars, altering their density across the landscape, with habitats that provide refuge from competition a limited resource in some landscapes. Cougars are better adapted to living near people than are wolves, which could result in increased concerns and conflict with humans, pets, and livestock in some areas.*

The ability of cougars to avoid direct competition in an ever-changing landscape of prey and competitors will be key to their coexistence with wolves, bears, and humans. Some research suggests that subordinate species are commonly displaced to marginal habitats (Woodroffe 2001), while cougars in Yellowstone exploited optimal habitats that provided refuge from competition but perhaps impinged on their foraging success in the long run. Within the Greater Yellowstone study area following the return of wolves, the spatial extent used by adult female cougars contracted by 10–46 percent, and for males the contraction was 43–65 percent. The direction in which cougars shift while trying to avoid competitors will likely be determined by the availability of complex terrain, heterogeneity of the landscape, and other habitat characteristics, such as areas of high human development and activity, which may limit use by wolves. Hence competition refuge habitats may be a limited resource for cougars in some landscapes.

When cougars seek refuge from competition, their numbers can increase locally in heterogeneous habitats that provide refuge. In the temperate Northwest, cougars concentrate on forested and rugged low-snow, low-elevation ungulate winter ranges, often along rivers and smaller riparian drainages. Outside protected and wilderness areas, these drainages are commonly roaded or otherwise developed, and this management structure tends to result in spatially clumped harvest in localized areas within management zones where human access is high (Beausoleil et al. 2013). While some habitats will harbor increased numbers of cougars and may initiate management action, a reduction of cat activity in some areas may be interpreted as marked declines in the management areas. Hence, depending on the

scale of management units, a view across a larger area and consideration of competitor density and habitat use are necessary. Hunting units that support cougars living with other large competitors can be managed adaptively through rest rotation, whereby periods of hunting alternate with periods of rest (Cooley et al. 2011). Lightly hunted areas may also serve as rest units, provided they produce a net emigration rate. Forest fire or development might further alter available refuge habitats, requiring consideration of adaptive, multi-species management approaches to mitigate impacts in areas with limited refuge and habitat for hunting prey.

In many places where cougars are hunted by humans, the competitive equation might be altered, as wolves and black bears are also typically hunted annually. Whether hunting moderates competitive effects or is additive to intraguild mortality for subordinate cougars remains a question. Long-term studies that assess competition in hunted and non-hunted multi-carnivore systems where prey are limiting and not limiting could help address this question, but existing information leans toward additive effects. Starvation was the second main cause of mortality following hunting mortality in the North Fork of the Flathead watershed, Montana, suggesting that competition may not be moderated by hunting when prey are a limited resource important to carnivores and hunters alike (Ruth 2004a). In areas with fewer or no wolves, hunting has been found to be additive to other sources of mortality for adults, subadults, and kittens, particularly when seasons and quotas are liberal (Robinson et al. 2008; Robinson and DeSimone 2011; Beausoleil et al. 2013; Wielgus et al. 2013).

Despite some degree of aversion by cougars to most human-related landscape features, cougars have nonetheless been relatively resilient to humans and their activities, especially compared to other large carnivores such as grizzly bears and wolves (Laliberte and Ripple 2004; Riley et al. 2004; Beier et al. 2010). In Banff National Park, Kortello and colleagues (2007) found that as wolf use increased during winter, cougars shifted to areas with relatively more human development and activity. On occasions when cougars range into populated areas, they are perhaps better at persisting in human-dominated landscapes than are more vocal and visible wolves. Cougars restrict themselves to areas of dense cover and typically are active when people are not (Sweaner and Logan 2009; Beier et al. 2010). The broad prey niche of cougars and their ability to take smaller prey may also give

them an advantage over dominant competitors, particularly in landscapes with more diverse prey than northern climates, thus enhancing their persistence in human-disturbed environments (see Núñez et al. 2000).

Although cougars are resilient and perhaps better able to persist in human-dominated landscapes than are other large carnivores, other outcomes might also occur, particularly in areas where ungulates can find good winter forage in fields adjacent to homes. Beier and co-workers (2010) speculated that interactions between cougars and populations of prey and other carnivores may be intensified in near-urban areas bounded by relatively impenetrable roads or development barriers. Others have also noted that in terrestrial ecosystems, strong interactions between mammalian carnivores and prey or competitors have been either on true islands (Peterson 1977; Terborgh et al. 2006) or in habitat islands created by urbanization or other human settlement (Crooks and Soulé 1999). Because landscape vegetation and irrigation around homes provides attractive forage for ungulates, warmer, drier climates that induce drought might also lead to landscaped yards becoming more attractive to elk and deer. Individual cougars that are relegated to seek prey in and around humans may face low human tolerance, making such places higher-risk areas for cougar survival.

As cougars and wolves naturally expand from their current populations, managers will face consideration of multiple carnivore species and changes resulting from interactions in their adaptive management plans. Driven by their impressive dispersal abilities, cougars have been on the move, with confirmed sightings accumulating in midwestern and eastern North America since about 1990 (Fecske 2006; Beier 2010; Cougar Network website, <http://easterncougarnet.org>). Wolves also are on the move, with individuals making it westward to Oregon and Washington and southward to Colorado. Their arrival may limit populations of subordinate species, or, conversely, long-established dominant species may hinder the probability of successful restoration (Johnson et al. 1996). Where and to what level cougars and wolves are restored in historical range will be a function of where people allow them to be and what habitats provide cougars with refuge from strong competition. As cats attempt to settle in well-established wolf areas such as Minnesota and Wisconsin, states could set the stage for management early in the process by proactively determining

areas that might support cougars, areas where conflicts are predicted, and public attitudes toward tolerance of cougars in various regions of each state.

- *Where they co-occur, large carnivores and humans compete with each other for prey. As they each select for a different age and sex cohort of elk or deer, their combined effects will at times be strongly additive to one another.*

Across regions where cougars, wolves, and bears currently occur, ungulates are economically important big-game species and an important target of management by wildlife agencies. As Peek (2010: 64) so aptly put it, "Reconciling management of large mammalian carnivores and the game they eat is where the rubber meets the road for the *North American Model of Wildlife Conservation*." Hunting by humans has contributed to the success of this model by generating funds that support wildlife management and habitat conservation within each state. Yet the goals of hunting ungulate game and sustaining carnivores continue to present challenges, as many people have traditionally believed that fewer carnivores mean more deer or elk.

Supporting our findings, research in other ecosystems has noted the important role body size of ungulates plays in determining the impact of predators—small ungulates experience stronger predation, whereas large ones experience greater food limitation (Jędrzejewska and Jędrzejewska 2005; Mills 2005). As a result, mortality switches from top-down in smaller prey species to bottom-up in larger ones, and a threshold in body size of around 150 kg has been suggested. Solitary hunting cougars are limited by prey size and almost exclusively select elk calves, which are important to recruitment and population growth, yet have low reproductive value. In the absence of other factors (competitors, drought), cougars alone seem ineffective at limiting the growth of large, healthy elk populations (Murphy 1998; Ruth and Murphy 2010). The coursing predation style of wolves imposes less of a limit on size, with greater emphasis on prey condition and age vulnerabilities. Wolves can limit large ungulate numbers but, like cougars, most commonly this occurs in combination with conditions that limit environmental carrying capacity and with multiple carnivores and humans (Bowyer et al. 1998, 2005; Hayes and Harestad 2000).

Whether killing of prey by cougars, wolves, bears, and humans is additive and exerts top-down forcing on prey appears importantly linked to the ratio of predators and

hunters to adult elk as well as calves, which are important for recruitment. But what might these magic numbers be? Prior to the arrival of wolves on the Greater Yellowstone Northern Range, cougars and bears numbered less than 6 per 1,000 total elk and ranged from 16 to 30 per 1,000 elk calves. After the arrival of wolves, cougars, bears, and wolves numbered 10 to 22 per 1,000 adult elk and were present at levels consistently above 50 carnivores per 1,000 calves at the point when calf recruitment dropped to 12 to 14 calves in 2001–2 through the remainder of our study. In other areas of Montana, where ratios of wolves and/or grizzly bears per 1,000 elk did not consistently exceed 4 to 5 per 1,000 elk, elk populations were stable to increasing (Hamlin et al. 2009a, 2009b). Although cougar densities were unknown, these data suggested that elk populations appeared to be able to sustain adequate recruitment with low levels of wolf and bear predation and moderate hunter harvest.

Also playing a role was migration of prey across boundaries, whereby the system was supporting multiple carnivores within Yellowstone National Park but subjecting them to human harvest outside Yellowstone. With the exception of 1987–88, numbers of hunter tags ranged from 23 to 200 per 1,000 adult elk. The timing and removal of elk by bears, cougars, wolves, and humans were not functionally redundant (i.e., did not substitute for one another; Kunkel 2003; Miquelle et al. 2005; Woodroffe and Ginsberg 2005). Instead, the predation effects of several carnivores combined to become additive sources of mortality for Yellowstone elk, and as the elk population and calf recruitment declined, the additive quality intensified. While sustained hunter harvest achieved reduction of elk numbers by 2004, an extended drought persisted at the same time (Cross et al. 2009; Hamlin et al. 2009a, 2009b; Smith and Bangs 2009).

This information underscores the fact that studies initiated in response to prey declines are short-term and focused on cause-specific kill rates. Without obtaining information on the physical condition and vital rates of prey, on climatic conditions, and on ratios of predators to prey, such studies are perhaps more likely to find that carnivores impose strong top-down limiting effects on prey (Bishop et al. 2009; Hurley et al. 2011; Pierce et al. 2012). Consequently, increased harvest of one carnivore species or several may be proposed. But such actions may have no discernible effect on ungulate declines until environmental effects on forage availability improve, at which time predation by cougars

and other carnivores may slow but not prevent recovery of ungulate populations (Pierce et al. 2012). The fact that Yellowstone elk did not begin to decline until almost ten years after wolf restoration while numbers of bears increased and hunting remained in place suggests that recovery from population lows may take longer, even if favorable climatic conditions prevail. As prey declined further, inter- and intra-specific competition for live and dead prey is predicted to increase, perhaps providing a mechanism that reduces predation as prey density decreases (Murdoch 1994; White et al. 2013). In this event, declining numbers of cougars and wolves should lag behind a decline in prey. Both a decline in growth of the cougar population in the final years of our study and a substantial decrease in the wolf population in 2009 and subsequent years as a result of intraspecific strife, disease, and food stress suggest that carnivores were responding to decreased availability of elk (Smith et al. 2011; White et al. 2013). Eventually, a decrease in the numbers of cougars and wolves should allow increased survival, recruitment, and abundance of elk under conditions that favor increased carrying capacity of the environment (White et al. 2013). Competition between carnivores, which may result in prey switching and apparent competition, further influences these complex associations. Determining benchmark ratios of carnivores to prey may require management treatments that include areas closed to hunting to understand the full spectrum of carnivore impacts without hunting as a source of mortality.

If, after consideration of ecological factors, the management objective is to reduce cougar numbers, killing males alone can lead to compensatory immigration of males from other areas, thus sustaining rates of predation on prey (Robinson et al. 2008; Cooley et al. 2009; Beausoleil et al. 2013). Killing adult female cougars in addition to males should have the greatest impact on reducing total predation rates because maternal females consistently have the highest kill rates and make up the largest proportion of resident populations. This management approach, however, needs careful consideration: it is unlikely to be favored by either hunting or non-hunting constituents because it results in frequent orphaning and starvation of kittens. In addition, removal of cougars, which typically occur at lower densities than wolves, might result in little effect on recruitment without other management actions, such as adaptive adjustments in hunter harvest of the target prey species.



## CLIMATE CHANGE AND CARNIVORE INTERACTIONS

- *Earth's climate is warming and changing. Forecasts of how the climate will change in the Greater Yellowstone Ecosystem suggest that the complex interactions among vegetation, prey, top-level predators, and scavengers will also change.*

Studies have already documented the effect of climate change on the reproductive success, distribution, and phenology—growth stages, such as flowering—of certain plants as well as effects on animals (see Walther et al. 2002). In the Rocky Mountains, regional projections of climate change suggest elevated temperatures, reduced winter precipitation, earlier spring runoff, and elevational shifts in vegetation zones, which could increase fire frequency and strip forests of moisture-dependent trees such as aspen (Neilson et al. 1989; Romme and Turner 1991).

Currently, two trends are apparent in the Greater Yellowstone Ecosystem. With midwinter snowfall decreasing, a declining trend in the date of the last snow on the ground, and an increase in the number of days with temperatures above freezing in January through March, winters on the Greater Yellowstone Northern Range have already become shorter (Wilmsers and Getz 2005). A projected larger nonforested area at low elevations could mean increased populations of ungulates in the Greater Yellowstone Ecosystem (Romme and Turner 1991; Wilmsers and Getz 2005). Milder and shorter winters and earlier green-up and access to new forage in spring would likely mean that elk will recover sooner from the detrimental stresses of winter. In turn, more rapid recovery of maternal condition lost over winter may contribute to improved growth rates and survival of calves.

Second, shorter winters mean that summers start earlier, and they are lasting longer, potentially corresponding to a decline in late winter elk mortality. Fewer winter-killed carcasses would affect species that are highly reliant on winter carrion for survival and reproductive success, including grizzly bears, black bears, coyotes, foxes, ravens, and bald and golden eagles. These species are frequent visitors to cougar and wolf kills and are more reliant on cougar- and wolf-killed prey when winter kills are less available. A pulse in carcasses associated with the narrower window of time over which carrion may be available is predicted to favor scavengers and competitors that can quickly detect and track food sources over great distances (Wilmsers and Getz

2005). Such conditions would favor detection of cougar kills by bears and wolves and would translate to increased kill rates of cougars, with potential survival and reproductive costs. Less forest at lower elevations might also increase habitat for foraging wolves and decrease suitable habitat for cougars, dependent on the amount and distribution of rough terrain in nonforest areas.

Warmer winters and drier conditions might also have other effects. Warmer temperatures and drought have resulted in earlier peaks in the growing season, followed by earlier curing of vegetation on higher-elevation grasslands, which could reduce forage quantity and quality. Poor-quality forage in late summer and autumn affects nutrition of migrant elk, resulting in increased probability of diminished calf growth and increased vulnerability of elk to predation in late winter (J. G. Cook et al. 2004). Such effects would enhance cougar and wolf predation on calves and further limit recruitment to the elk population.

How climate change affects not only the vulnerability of elk and carcass distribution but also seed-producing whitebark pine could have additional influences on subordinate competitors. About 30 percent of productive whitebark pine habitat was burned in the 1988 Yellowstone fires (Knight et al. 1999). Following fire, the natural regeneration of whitebark pine takes close to fifty years, and significant cone crops typically are not produced until trees are sixty to eighty years old (Krugman and Jenkinson 1974; Knight et al. 1999). Sweltering summers and dry winters potentially complicate the effects of fire (frequency, size, and intensity) and affect successional replacement, and they may lead to accelerated rates of spread by invasive white pine blister rust (*Cronartium rubicola*) as well as increased impacts from native mountain pine beetle (*Dendroctonus ponderosae*; Romme and Turner 1991; Mattson et al. 2001; Schrag et al. 2008). The long-term effects of reduced cone-producing whitebark pine trees may affect grizzly bear foraging, especially during years when alternate native foods are also in short supply (Knight et al. 1999). Any alterations to or reductions in summer and fall forage could affect pre-hyperphagia accumulation of adipose reserves, and some bears may forage on carrion during milder winters (Servheen and Cross 2010).

We suspect that cougar-killed prey would increase in importance in fall in light of milder winters and declining whitebark pine seed crops because bears rely more heavily on carrion in years of poor whitebark pine seed crops

(Mattson et al. 1991, 2001; Knight et al. 1999; Schwartz et al. 2013). Further, fewer winter-killed carcasses available in springs following mild winters would be additionally costly to cougars because fewer spring carcasses increase the odds that bears will displace a cat from its kill. Wolves have increased the amount of carrion available to scavengers, and they may buffer the effects of climate change on carrion availability in the future (Wilmers and Getz 2005). We found a doubling in visitation and displacement of cougars from their kills during wolf presence compared to before wolves. Increased bear numbers probably played a role, yet the rate of displacement during wolf presence also hinged on the increased proportion of large prey killed by cougars, as the ratio of calves to cow elk trended toward fewer calves. Hence exploitation competition for fewer calves might cascade to increased interference competition for large carcasses, resulting in increased energetic costs that influence cougar survival. The fact that cougar and wolf kills differ in distribution across the Greater Yellowstone Northern Range is also important to consider. The resulting increased amount and wider distribution of carrion than in a wolf- or cougar-only system provides resources that are more dispersed and do not concentrate local scavenger communities (Wilmers et al. 2003a, 2003b).

Intact food webs that include top predators may be more resistant to stress, such as changing climate (Wilmers et al. 2002). If so, increasing our knowledge of the number of species and the time of year they rely on carrion or how changes in the distribution of carrion affect these species also seems beneficial to predict the effects of a warming climate on multiple species. Collaborative efforts across disciplines would result in more extensive knowledge and enable methods, funding, and other resources to be pooled (Wilmers and Getz 2005). Coming together to address landscape impacts from climate change, land use change, and invasive species, a planning committee composed of land managers, experts within disciplines, and interested-party observers recently helped develop a science agenda for the Greater Yellowstone area (Olliff et al. 2010).

## SUSTAINING FUNCTIONING POPULATIONS, ECOLOGICAL PROCESSES, AND RESILIENCY

- *Naturally low turnover of individuals and stable social relationships are life-history characteristics that impart beneficial traits to offspring, help cougars defend and provision offspring, and benefit*

*the mother through increased vigilance by growing young, all of which may be adaptive for surviving in competitive environments.*

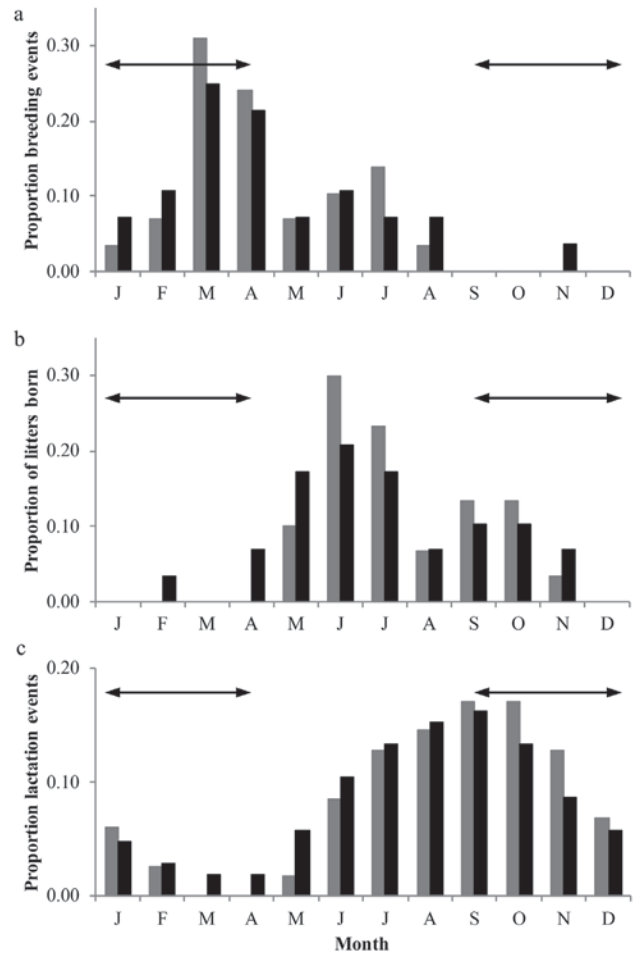
Protecting the inherent natural resiliency of cougars and other carnivores may be one of the most important conservation steps in light of habitat fragmentation and a changing climate (Weaver et al. 1996). As Logan and Sweanor (2010: 117) sum up, "This view of cougar social organization as a template for adaptations that maximize fitness, with different male and female behaviors that maximize individual survival and reproductive success, throws into sharp focus the need for wildlife managers to consider the influence of human selection pressure of all kinds upon the ability of cougars to adapt to changing environments."

Cougars are long-lived species that develop and maintain relationships with neighbors. Cougar population growth and resiliency are reliant on the survival of females to provide long-term care that enhances offspring survival in competitive environments, which may also benefit the mother through increased vigilance of her growing young (see also Logan and Sweanor 2010). Tenure of territorial males also has important implications for individual reproductive success, as well as for delivering to offspring beneficial traits that may be lost when turnover of males is frequent (Murphy 1998). Frequent removal of males and the consequent immigration of new males contribute not only to increased infanticide in some areas but also to mortality of female cougars—resulting from aggressive interactions with immigrant males while protecting offspring or during mating (Logan et al. 1986; Logan and Sweanor 2001; Cooley et al. 2009; Ruth et al. 2011). We linked less stable social relationships between cougars (present prior to wolves) to larger home ranges, kill rates that reflected energy-maximizing and time-minimizing strategies, and infanticide of kittens. Because cougar harvest in most northwestern states occurs prior to and overlapping the primary breeding season of cougars in late winter, removal of adults might result in a resorting of survivors, resulting in infanticide heightened during winter breeding, as we documented in our PW study (fig. 18.1a; Ruth et al. 2011). In other studies kitten survival was reduced as a result of orphaning following hunting, not from increased infanticide (Cooley et al. 2009; Packer et al. 2009; Robinson and DeSimone 2011). If cougars with the greatest ability to survive and produce offspring in wolf-dominated landscapes are consistently removed through hunting, cougar population growth and contribution to

surrounding areas might be substantially altered over the long term.

Breeding during late winter and spring and giving birth to kittens when food is abundant in early summer may be particularly important in northern climates, as kittens enter winter at younger ages and lower body mass could be compromised when trying to keep up with the mother and when fleeing from competitors in deep snow. Timing of hunting that precedes and overlaps late winter–early spring breeding might alter timing of births, affecting offspring survival later on (fig. 18.1b). Whether breeding and hence births occur later in hunted areas compared to what might be typical in primarily non-hunted populations is not clear. Two other northern cougar studies, reflecting heavily hunted areas, reported a single birth peak across the months of July through October, only slightly later than the primary birth peak in our study (Ross and Jalkotzy 1992; Robinson and DeSimone 2011). Hunting regulations in many states already restrict harvest of females with kittens by their side or lactating females. Given that female cougars support dependent young for 65–82 percent of their reproductive life, they are frequently together. Yet kittens that are twelve months old or younger may travel with their mothers as little as 19–43 percent of the time, reducing the likelihood that they are detected (Barnhurst and Lindzey 1989). Determining that a female is lactating is also not an easy prospect, and many mothers may no longer be suckling kittens when hunting begins (fig. 18.1c). Hunters who encounter adult female cougars (greater than twenty-four months of age) should suspect that the cats are supporting dependent offspring.

Lastly, females with kittens kill prey more frequently than do solitary females and males; thus the potential for detection and displacement by other carnivores is greatest for family groups—as is the potential for injury or death during interactions. When a kill is lost to another carnivore, the family is tasked with making another kill in short order—more quickly than if they had reaped calories from the kill. During hunting and dog training seasons, hunters, too, may frequently displace females from kills, which could have energetic costs during more severe winters and in areas with greater road access. Research programs that use hounds might also contribute to cougars abandoning kills, particularly where they overlap areas in which cougars are hunted and where they are sympatric with other large carnivores. Information on displacement of cougars from kills by com-



**FIGURE 18.1.** Timing of combined hunting seasons for cougars in Idaho, Montana, and Wyoming (arrows) relative to the (a) breeding, (b) birth, and (c) lactation chronology of cougars on the Greater Yellowstone Northern Range, 1987–2005. Gray bars are pre-wolf; black bars are during wolf breeding, birth, and lactation chronology.

petitors as well as by hunting and research activities would broaden understanding of the costs to cougars, their rate of killing, and thus influences on prey species.

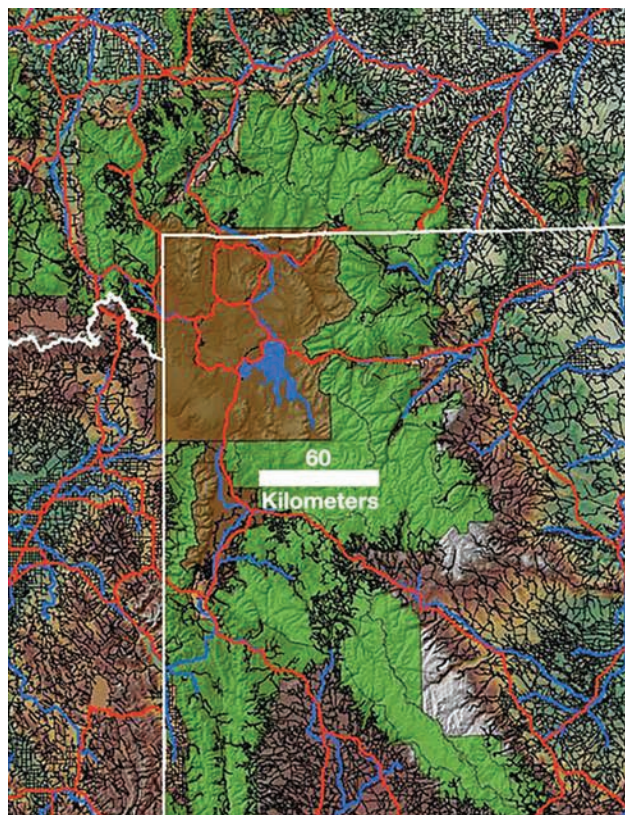
- *Functional and effective dispersal is a key mechanism for persistence and resilience of cougar populations, but at times it may be moderated by dominant competitors.*

Because carnivore numbers will not be strongly influenced by humans within protected areas (Schullery 2010; White et al. 2013), protected landscapes may be where competition between carnivores plays out most robustly. Cougars



are subordinate competitors, so there are likely to be times when they become limited through competition for limited resources, such as fewer prey. This might translate to periods when their contribution of individuals to the surrounding mega- or meta-population wanes, as recovery of the local population within the park should occur most strongly through philopatric daughters and immigration. During such times the Northern Range cougar population may more strongly depend on ingress from outside park boundaries (i.e., dependent source in Newby et al. 2013).

Without gene flow from emigrants to new areas, cougar populations could be unable to adapt to altered environmental conditions, competition, or diseases, hence losing their resiliency (Logan and Sweanor 2001). Overall, the dispersal capabilities of cougars make them good candidates for persistence, as is growing more apparent as they make their way to midwestern states (Beier et al. 2010; Quigley and Hornocker 2010). Having as few as one to four immigrants into small populations greatly increases the probability of persistence within the small population in a 100-year projection (Beier 1993). While smaller protected areas would appear most susceptible to the effects of roads, development, and adjacent high-mortality landscapes that create a “fence effect” and limit dispersal, such effects are also noticeable in the Greater Yellowstone Ecosystem (fig. 18.2; Woodroffe and Ginsberg 1998; Hansen 2009; Schwartz et al. 2010; Newby et al. 2013). To the north of Yellowstone, Interstate Highway 90 has existed for decades, and it is a plausible physical barrier—or at least an impediment—to cougar movement (Wheeler et al. 2010). Hence gene flow in the Greater Yellowstone area may be greatest in a north-south exchange with Grand Teton National Park and an east-west exchange across the Absaroka-Beartooth Mountain Range and Sunlight Basin in Wyoming. In both Yellowstone and the Garnet Range of Montana, lower overall survival rates for male dispersers and greater dispersal distances for females may indicate that females contribute more to interpopulation exchange than do males in areas where they are subject to high hunting mortality (Newby et al. 2013). Consequently, even in Greater Yellowstone, it may be worth considering how to maintain linkages to habitats that act as “stepping stones,” enabling greater exchange between more distant populations. With their productivity and dispersal capability, cougars might respond adequately to refugia that are well distributed in several units across the landscape at distances



**FIGURE 18.2.** Yellowstone National Park (brown within black boundary) functions as an important, viable source population of cougars that contributes emigrants to the surrounding Greater Yellowstone Ecosystem. While much of the area may be permeable to movement by cougars, high-mortality landscapes around protected areas such as Yellowstone might create a “fence effect,” limiting dispersal and the refuge’s ability to act as a source that links to more distant habitats. Roads (right, shown in red and black) influence this fence effect. For example, increased road density negatively influences cougar survival, enabling greater hunter access during winter. Interstate Highway 90 to the north of Yellowstone is a plausible biological barrier—or at least an impediment—to cougar movement.

scaled to successful dispersal (e.g., less than five home range diameters proposed by Weaver and colleagues [1996] and perhaps less than three diameters where heavy hunting limits effective dispersal [Newby et al. 2013]). Broader efforts are needed to understand gene flow between areas, which can be accomplished with existing and developing genetic sampling methods and technologies.



- *The number and distribution of carcasses resulting from predation by cougars, wolves, and other large carnivores contribute important nutrients within the ecosystem, supporting a diverse array of other species. Some are reliant on carcasses to get them through tough winter times, whereas the life cycle of others is tied to decomposing carrion.*

Carnivores importantly influence ecosystem function by depositing carcasses across the landscape (Bump et al. 2009a, 2009b). In chapter 7 we touched on the number of carcasses—between 1,210 and 2,036 annually—distributed across various portions of the Greater Yellowstone landscape as a result of predation by cougars and wolves combined, as well as the importance of these carcasses to scores of other species. Carnivores initiate the process of breaking down the carcasses of animals they kill, which is important for ravens, magpies, and other avian species because they are limited in their ability to tear open a carcass to feed (Heinrich 1988, 1989; Stahler et al. 2002). Each species that feeds on a carcass may further distribute the nutrients by transporting chunks of meat and stashing them elsewhere (magpies, ravens) and through defecation. Carcass-derived nitrogen inputs lead to higher available nitrogen in soils, resulting in increased plant nitrogen assimilation (Bump et al. 2009a, 2009b). Even carcasses that are mostly consumed by carnivores produce substantial resource “hot spots” in forests and grassland soils, with effects on belowground communities and aboveground producers (Bump et al. 2009 a, 2009b). Carcass-derived nutrients can be used in plant growth for three growing seasons postmortem, which then influences aboveground trophic interactions as large herbivores are attracted to patches of nitrogen-rich forage (Danell et al. 2006). This means that carcass sites become foraging sites, and the probability of repeated foraging within and around carcass sites initiates a positive feedback of recurrent nutrient supplementation from feces and urine deposition (Towne 2000; Bump et al. 2009 a, 2009b).

Although human hunting, wounding loss, and vehicle collisions may contribute more carcasses than do carnivores, contributing to nutrient pulses, these carcasses and gut piles produce super-abundant pulses and with less dispersion than wild predator kills (Wilmers et al. 2003b; Bump et al. 2009b). Clumping of carcasses along roadsides already occurs as a result of widespread vehicle collisions with large ungulates (Romin and Bissonette 1996). Carcasses near roads are detected by diurnal scavenging raptors much faster

than those far from roads, and eating near roads makes birds vulnerable to collision and to being hunted, especially large species that are slow to take off (Lambertucci et al. 2009). In contrast, cougars and wolves hunt continually across a wide range of habitats, resulting in carcasses distributed in various forested and grassland microsites at a rate that differs from the rates and distribution of carcasses from other causes of mortality (Wilmers et al. 2003b; Kauffman et al. 2007). Cougars most typically hide their kills near the base of a tree, likely providing a pulse of nutrients important for tree growth, while wolf kills leach nutrients important to grasses, sagebrush, and other vegetation in more open habitats. Loss of predation and the resulting loss of carcasses could substantially reduce the distribution and consistency of this important food and nutrient source and in turn may compromise ecosystem function and resilience.

## CONCLUDING THOUGHTS: CONTINUING COEXISTENCE

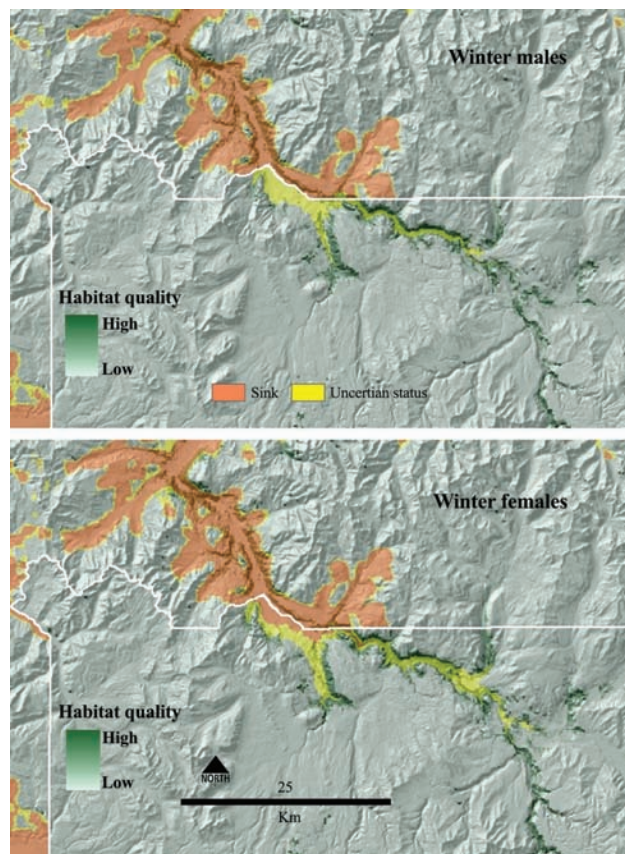
Humans can choose to coexist with large carnivores by providing large landscapes that serve as refuge from competition, enabling cougars and other carnivores to operate as functional breeding populations for the long term. Maintaining large protected areas through zone management, or a source-sink management approach, enables intricate, dynamic relationships between species to play out, such as carnivory, scavenging, and interspecific behaviors (Logan and Sweanor 2001; Laundré and Clark 2003; Mills 2005; Stoner et al. 2006; White et al. 2013). In this way large protected areas also serve as incubators of experience and knowledge; the areas help maintain traits that enhance survival in competitive environments, allowing for the expression of the full evolutionary potential of many species (Mills 2005; Ray et al. 2005; White et al. 2013). But are they alone enough to support migratory prey populations, multiple large carnivores, and adjacent human influences?

Within source-sink or zone management structure, management plans for large carnivore guilds could benefit from (1) identifying habitats that provide refuge from competition for multiple carnivores within and outside protected areas, (2) determining whether additional protections for migratory prey outside protected areas are beneficial, and (3) periodic, multi-party monitoring of source populations and linkages, using science and engaged citizens, to evaluate connectivity effectiveness across large landscapes.

### Identifying Habitats That Provide Refuge

Even within protected landscapes, habitat that provides sufficient refuge limits where cougars can be, potentially resulting in a contraction of available habitat when dominant competitors are part of the picture. Identification of refuge habitats needs consideration in areas managed for multiple large carnivores and their migratory prey. Questions can first be developed that help address gaps in information. Where do habitats that provide refuge lie within management units and management zones? During winter, are they situated across park or other management boundaries where prey migrate but management approaches may vary? Are greater road densities present in those areas that provide refuge? When we mapped source-sink structure for the Greater Yellowstone Northern Range by combining our habitat models and population data, areas inside the park and wilderness did serve as important source habitat. But during winter quality habitat was limited, and low-elevation areas both inside and outside the park were potential sinks (fig. 18.3; Ruth et al. 2011).

While managers often do not have the data to incorporate wolf and prey use to evaluate and map habitat and to incorporate survival at the level we did, such data are accruing from various studies throughout the West, enabling opportunities to incorporate habitat on broad scales into management plans. New approaches have also developed in which available cougar habitat is incorporated with estimated cougar densities to predict population size within smaller management units as well as across larger cougar management zones (Beausoleil et al. 2013; Robinson et al. 2015). When estimates of mortality and dispersal are incorporated, these tools enable predictions about the effects of harvest management decisions on cougar population dynamics (Robinson et al. 2015). Because they might underestimate the size, types, and attributes of landscapes necessary to ensure comprehensive conservation benefits, single-species approaches may be inefficient when it comes to developing, monitoring, and evaluating the success of multiple species management and habitat conservation plans (Barrows et al. 2005; Kunkel et al. 2013). To bridge this gap, Barrows and colleagues (2005) proposed a hybrid approach that employs conceptual and spatial data in an iterative process to create niche models for species and species associations within natural communities. Such spatially explicit conceptual models incorporate hypotheses about habitats, processes, landscapes, and threats to the integrity



**FIGURE 18.3.** Source and sink structure for male (top) and female (bottom) cougars during winter on the Greater Yellowstone Northern Range. We mapped habitat quality in source and sink areas for the during wolf period using the most supported individual synoptic habitat models (chapter 11). We fixed snowpack, elk use, and wolf use attributes to represent the means experienced during the winter across all years of the during wolf period. For females, source areas were defined as survival greater than or equal to 0.93 and sinks as survival less than 0.93 (Ruth et al. 2011). For males, source areas were defined as survival greater than 0.71 and sinks as survival less than 0.47, with survival between 0.47 and 0.71 classified as unknown status. Habitat quality was overlaid on these survival definitions for a visual display of habitat quality in source and sink areas.

of each of these components that dictate species occupancy within a habitat matrix. Hypotheses can then be applied in a predictive manner to a landscape over the entire region of interest (Barrows et al. 2005). We propose that data on cougars, wolves, grizzly bears, prey, and other species could be used in such a process to develop, corroborate, and apply multi-species niche models in a predictive manner across

the Greater Yellowstone Ecosystem. Measures of landscape heterogeneity can be included in the process. Heterogeneous landscapes should allow for more stable coexistence of cougars and wolves, as the existence of habitats less frequented by wolves affords cougars some refuge from competition. The resulting multi-species niche models could then be adapted, tested, and modified elsewhere, ultimately identifying not only the areas in need of greater monitoring of species occurrence and abundance but also the anthropogenic and natural environmental drivers in specific areas. The focus on environmental drivers supplies managers with direct information as to how, when, and where to employ adaptive management strategies (Barrows et al. 2005).

### **Considering Prey Movements and Roads: Are Additional Protections Warranted?**

Boundaries of a majority of existing protected areas were not established with consideration for the migratory nature of ungulates and carnivores. On their own, most protected areas are not large enough to sustain predator-prey-scavenger associations and other biological processes fully; even Yellowstone National Park, almost 9,000 km<sup>2</sup> in size, is not large enough for this (Woodroffe and Ginsberg 2000; Cegelski et al. 2004; White et al. 2013). Where we are committed to sustaining secure populations of coexisting species over the long term, management actions in surrounding zones should take into account how functional the protected areas are and should strive to support their integrity (see also Mills 2005).

Where populations of multiple carnivores and multiple prey species are deemed essential source populations—helping to buffer against a changing human landscape and climate change and maintaining gene flow—consideration of how they use adjacent landscapes could reveal whether additional protections are warranted. This may take some work, as agencies under differing management mandates find difficulty reaching consensus on how to provide for functioning ecological processes (dispersal, migration, predation) or conservation of species surrounded by controversy and conflict with humans (e.g., wolves, bison, wolverine—White et al. 2013). Unless we physically transport individuals between habitat patches, carnivore populations will struggle to survive if we lose the landscape connectivity that enables movement across large areas. Endangered Florida panthers provide a good example of where genetic exchange was

insufficient, resulting in inbreeding effects, and intervention through introduction of individuals from Texas was deemed necessary to preserve the population (Johnson et al. 2010). In Yellowstone, even after cougars were constrained to winter habitat that totaled 816 km<sup>2</sup> during wolf presence—around half the size of winter habitat in the PW period—the cougar population functioned primarily as a net contributor, or source population, to adjacent areas (chapter 16; Newby et al. 2013). Protecting as little as 12 percent of winter range—an area of 915 km<sup>2</sup>—from hunting during winter was sufficient to transform one area from a population sink to a viable population source for cougars in Montana (Robinson and DeSimone 2011). Ultimately, the protection of small areas does not guarantee positive or stable growth rates, as the size is also reliant on surrounding source productivity and sink mortality structure, and each source needs to be linked to other cougar habitats.

Prey species that migrate from protected areas, where they serve as essential food for multiple carnivores, to low-elevation winter range outside protected areas, where they are hunted by people, are subject to mortality that affects all age classes, which can be strongly additive. Incorporating existing prey winter ranges and road density when identifying refuge habitat within high-mortality landscapes should help highlight where protection falls short. Expansion of protected area boundaries is rarely an easily implemented management option, but where maintaining migratory processes is warranted, state agencies might consider greater protection of prey on critical winter ranges. Adaptive, restoration strategies described earlier in this chapter might be particularly beneficial, distributing human harvest in ways that provide greater protections near source areas for some periods of time and less so during others.

### **Carnivores and Large Landscapes: Periodic Monitoring and Citizen Partnerships**

Science will play an important role in the process of addressing ongoing and emerging management and conservation challenges, but so, too, must an engaged citizenry (Logan and Sweanor 2001; Sillero-Zubiri and Laurenson 2001; Schullery 2010). The management of large carnivores and their prey takes place in complex and locally variable contexts, and in many places there is deep care for wildlife and the legacy we leave to future generations. Private, public, and agency partnerships may be the future for effective multi-species



management, considering the various stresses—such as habitat fragmentation, climate change, fire, and the reliance of local economies on surrounding natural resources. Because local communities can be strong and vocal advocates for wildlife and are often interested in new information about cougars, they should be included in discussions about factors that increase the resiliency of cougars in the face of myriad stresses. Already, the top-down approach to wildlife management has been changing toward effective bottom-up approaches: approaches in which scientists, agencies, and interested citizens sit at the table—or walk in the field—together to address local community, county, regional, and larger landscape issues. For instance, a wildlife summit held in 2012 by the Idaho Department of Fish and Wildlife was hugely successful at engaging citizens in a discussion about the future of wildlife management in the state, with overwhelming support for the conservation of all wildlife as an important part of Idaho's legacy for future generations.

Any multi-species management and conservation efforts will benefit from periodic monitoring. Periodic monitoring—perhaps at three- to five-year intervals—would provide the necessary regular reviews at the status of source populations as well as population structure across larger spatial scales (Sinclair et al. 2001; McRae et al. 2005). Again, partnerships can provide the greatest opportunity to monitor multiple species across boundaries. Growing out of a desire to overcome gridlock and better address multiple needs and concerns, collaborative resource management and multi-party monitoring (such as through forest restoration collaboratives) have already proven to be successful models for addressing local and regional issues (e.g., visit <http://www.salmonvalley.org/forest-restoration/>; Maehr et al. 2001; White et al. 2013). We direct readers to Susskind and colleagues (2012) and Moote (2013) for tools and strategies collaborative groups can use to develop and evaluate their work.

The effectiveness of existing habitat linkages, detection of barriers from future human development, and detection of excess mortality can also be accomplished through periodic monitoring. Yellowstone National Park already monitors wolves and grizzly bears, as do many other protected areas. Cougars present more difficult challenges, but genetic samples can be obtained through partnerships involving hunters, non-hunters, and children in citizen science projects to collect DNA and other data; such data gathering not only advances research and management needs but also fosters greater understanding of cougar biology and engages local communities in management decisions (Koehler and Nelson 2003; Beausoleil et al. 2005; Robinson and DeSimone 2011). New models using genetic identification offer promise for estimating population size for multiple species (e.g., spatially explicit mark-recapture, or SECR, models, Russell et al. 2012). Hunters must also check carcasses of cougars and other wildlife at hunter check stations or area offices of state agencies. Such checks provide opportunities to collect biological samples, including tissues for extraction of DNA; reproductive tracts; blood and tissue samples or swabs for assessing prevalence of disease, parasites, and exposure to human-produced contaminants (e.g., mercury, pesticides); gastrointestinal tracts for assessing prevalence of internal parasites; and age and sex of animals (Whittaker and Wolfe 2011). Ultimately, these data can assist managers in determining if a population is suffering from a bottleneck, inbreeding, or other stress, necessitating greater conservation efforts (Cegelski et al. 2004; Culver and Schwartz 2011). Whether we hunt or not, we can contribute to conservation in financial and various other ways. All who are passionate about wildlife and concerned about the future of natural systems and particular species in our changing world should be doing whatever we can to support the agencies charged with wildlife management and conservation.



## APPENDIXES



## APPENDIX A

### Kill Evaluation and Categorization Chart (November 10, 2000)

#### LIST NUMBERS THAT APPLY ON PREY CARCASS FORM

##### Carnivore Kill:

1. Sign of struggle evident
  - a. Scuff or track evidence of chase and struggle
  - b. Blood and hair on ground from pursuit
  - c. Broken branches
  - d. Blood on trees
2. SubQ hemorrhage on hide/carcass
3. Aspirated blood in trachea, mouth, nose

| Carni-<br>vore | Possible                                                                                                                                                                                                                                                                                                                                                                                                                                                             | Probable                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      | Positive                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
|----------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Cougar         | <ol style="list-style-type: none"><li>4. Old cougar trx. discernible by shape and stride pattern only.</li><li>5. Ungulate prey hair in small "clumps" around carcass has appearance of being sheared off or cut near root base.</li><li>6. Feces covered in "toilet" but dry or chalky in appearance.</li><li>7. Toilets, scrapes, bed sites not apparent or appear "weathered."</li><li>8. Carcass remains in dense cover, small drainage, or side draw.</li></ol> | <ol style="list-style-type: none"><li>9. Fresh cougar tracks discernible by detailed toe and pad arrangement.</li><li>10. Carcass remains concealed near tree and/or brush.</li><li>11. Carcass remains not scattered but clustered in area &lt;30 m.</li><li>12. Remains buried/cached w/ light debris such as plucked hair, small sticks, leaf-needle-soil duff. During winter, caches may be snow-packed, completely covering the top of the carcass.</li><li>13. Cougar feces dark, moist, or liquid.</li><li>14. Toilets and/or scrapes appear recently created.</li><li>15. Tree scratching at site</li><li>16. Two-four bed sites oriented upslope from carcass and concealed at base of tree, against boulder or rock outcrop.</li><li>17. Bed sites contain cougar hair.</li><li>18. Rumen rejected as food, possibly buried/cached.</li><li>19. Presence of cougar via visual, tracks, or radio-location.</li></ol> | <ol style="list-style-type: none"><li>20. Canine punctures to back of neck or at throat.</li><li>21. Hemorrhage to back of neck or at throat near jawline.</li><li>22. Claw marks or claw tracks apparent along neck, shoulders, back, or face.</li><li>23. Drag marks to cache/concealment site with ungulate prey hair along drag line.</li><li>24. Kill not scavenged by bear or wolf.</li><li>25. Canine holes measure 4.5 to 5.7 cm apart for top canine punctures and/or 3.0 to 4.5 cm apart for bottom pair.</li></ol> |

*continued on next page*

| <i>Carni-<br/>vore</i> | <i>Possible</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           | <i>Probable</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  | <i>Positive</i>                                                                                                                                                                                                                                                                                                                                                                                                                                  |
|------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Wolf                   | <p>26. Old wolf trx. discernible by shape and stride pattern only.</p> <p>27. Carcass remains in open habitat with &lt; canopy cover.</p> <p>28. Feces in open and not covered; feces dry or chalky in appearance; or no feces present at all.</p>                                                                                                                                                                                                                                                        | <p>29. Fresh wolf tracks discernible by detailed toe and pad arrangement.</p> <p>30. Carcass remains scattered possibly &gt;300 m from the kill site.</p> <p>31. No bed sites evident.</p> <p>32. If bed sites evident, generally more than two–four bed sites oriented in “spoke-wheel” fashion around kill site; bed sites in open on grass or under canopy cover but not necessarily at base of tree.</p> <p>33. Bed sites contain wolf hair.</p> <p>34. Radio-collared wolves at or in vicinity of kill.</p>                                                                                                                                                                                                                 | <p>35. Hemorrhage apparent on hide at back of metatarsus and femur areas.</p> <p>36. If any hide or organs left to examine on head at throat: canine punctures to throat on cows and calves.</p> <p>37. No cougar or bear sign at site.</p> <p>38. Canine holes measure 4.5 to 5.3 cm apart for top canine punctures and/or 3.0 to 4.0 cm apart for bottom pair.</p>                                                                             |
| Bear                   | <p>39. Old bear tracks discernible by shape or as depressions in soil only.</p> <p>40. Carcass may be in open (generally grizzly bear) or forest cover (generally black bear).</p> <p>Note: Bears in Yellowstone scavenge carcasses (winter kill, cougar and wolf kills) during spring, so make sure no other carnivore sign is evident at the site. Bear predation in YNP is generally directed at calves and fawns, where most of the carcass is entirely consumed, or bison kills (grizzly bears).</p> | <p>41. Recent bear tracks that show track details.</p> <p>42. Moist/wet bear scats in vicinity or on outer perimeter of bed sites.</p> <p>43. Bed sites within meters of carcass or next to carcass.</p> <p>44. Bed sites contain bear hair.</p> <p>45. Grizzly or black bear hair on antlers, trees, or brush.</p> <p>46. Carcass buried with large amount of material, including large sticks and dirt; area as churned or roto-tilled appearance indicative of grizzly bear.</p> <p>47. Carcass in tree cover or draw but not cached—more indicative of black bear.</p> <p>48. Hide on carcass is inverted over the head and down the legs, resulting in a “banana-peel” appearance.</p> <p>49. Viscera consumed as food.</p> | <p>50. Bear sign only; no other cougar or wolf sign present.</p> <p>51. Broken neck-rift on occipital condyle/cervical vertebrae.</p> <p>52. Extensive bruising on back of hind quarters, ribs, and/or shoulders.</p> <p>53. Bite marks to spine behind shoulders.</p> <p>54. Canine puncture holes measure 5.5 to 6.5 for upper canines and 5.5 to 6.5 for lower canines for grizzly bears and 4.5 to 5.5 for lower canines on black bears.</p> |



## APPENDIX B

### Modeling Factors Influencing Kill Rates

We used Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ) and the difference in  $AIC_c$ ,  $\Delta AIC_c$ , and model weights to compare models and determine which model or models were best supported by the data (Burnham and Anderson 2002). We further evaluated models with a difference in AIC of less than three. We assessed the precision of the slope parameter,  $\beta_i$  estimate, of the best approximating model(s) based on whether the 95 percent confidence interval (95% CI) for each covariate  $\beta_i$  overlapped zero (Graybill and Iyer 1994). Those not overlapping zero provided clear evidence of the direction and magnitude of effect, while those overlapping zero were difficult to interpret and did not support a clear direction and magnitude of effect.

#### ASSESSING MULTICOLLINEARITY

We first produced a correlation matrix as our starting point. Variables with  $R^2$  greater than 0.50 may indicate multicollinearity, but assessing tolerance (multiple regression with each independent variable as dependent variable) detects multicollinearity. We use a common tolerance cutoff of  $\leq 0.1$  and a variance inflation factor of  $< 3$  as indication that two

variables were not correlated (Zuur et al 2007), as shown in the following table:

| <i>Variable</i> | <i>R<sup>2</sup></i> | <i>Tolerance</i> | <i>VIF<sup>1</sup></i> |
|-----------------|----------------------|------------------|------------------------|
| PRE-WOLF        |                      |                  |                        |
| Calf biomass    | 0.489                | 0.511            | 1.958                  |
| Temp            | 0.361                | 0.639            | 1.564                  |
| Cougar density  | 0.273                | 0.727            | 1.376                  |
| Weight          | 0.268                | 0.732            | 1.366                  |
| AM density      | 0.232                | 0.768            | 1.301                  |
| Elevation       | 0.222                | 0.778            | 1.285                  |
| F:M ratio       | 0.027                | 0.973            | 1.027                  |
| DURING WOLF     |                      |                  |                        |
| Elk pop         | 0.649                | 0.351            | 2.849                  |
| AM density      | 0.178                | 0.822            | 1.217                  |
| Cougar density  | 0.139                | 0.861            | 1.161                  |
| Weight          | 0.131                | 0.869            | 1.151                  |
| Elevation       | 0.127                | 0.873            | 1.145                  |
| Wolf pop        | 0.125                | 0.875            | 1.143                  |
| Calf biomass    | 0.122                | 0.878            | 1.139                  |
| Wolf use        | 0.051                | 0.949            | 1.054                  |

<sup>1</sup> VIF = Variance inflation factor.

## APPENDIX C

### Fixed Kernel Home Range Estimation and Smoothing

Kernel methods of home range estimation use a smoothing parameter or bandwidth ( $h$ ) to estimate the degree of uncertainty or spread around each location. The fixed kernel method we employed uses the same bandwidth across the entire home range. A low value of  $h$  gives the estimate a small value of spread around each point and a more variable (under-smoothed) home range, whereas a high value of  $h$  has the opposite effect. Several methods have been proposed to calculate an optimal smoothing factor. The fixed kernel estimator with bandwidth chosen using cross-validation yielded the most accurate estimates of home range areas and had the smallest variance (Seaman et al. 1999). Yet the popular use of the least squares cross-validation (LSCV $h$ )

method for selecting  $h$  can over-smooth and create highly fragmented home range estimates, especially when sample sizes are small or very large or when several locations are at or near the same point (Kernohan et al. 2001; Horne and Garton 2006b). Another option is a reference smoothing factor ( $h_{\text{ref}}$ ), which assumes a bivariate normal distribution and often results in over-smoothing. The bandwidth we used was chosen with the *cvc- $h$*  option in Horne and Garton's (2007) Animal Space Use Program (V1.2, [http://www.cnr.uidaho.edu/population\\_ecology/animal\\_space\\_use.htm](http://www.cnr.uidaho.edu/population_ecology/animal_space_use.htm), accessed September 15, 2008), which provides a smoothing option that is generally larger than the LSCV $h$  and smaller than  $h_{\text{ref}}$ .

## APPENDIX D

### Population-Level Estimates of Selection Coefficients

We ranked models and compared the set of models following Burnham and Anderson's (2002) guidelines for the use of AIC values to assess support from the data for each competing model, with Akaike model weights ( $w_i$ ) used to address model selection uncertainty. This approach quantifies the tradeoff between obtaining a good fit to the data and avoiding overparameterization (Burnham and Anderson 2002). Also following Burnham and Anderson (2002), our final model was a weighted average of the set of top models. We also compared the 95 percent confidence intervals of each variable to evaluate if the coefficients were statistically different between the PW and during wolf time periods.

A critical component of the synoptic model was the ability to incorporate the effects of temporally varying covariates (e.g., snow cover, elk and wolf use). Model parameters were estimated via numerical maximum likelihood and used to infer both the magnitude and direction of influence of each covariate. Information theoretic criteria were used to identify a set of model covariates to include for predicting space use. We developed synoptic models for each individual cat and defined our top model set to include those models for which Akaike weights summed to  $\geq 90$  percent of all possible model weights (Burnham and Anderson 2002). We also assessed the relative importance of each variable by summing the Akaike weights across all models in the top set where a given variable occurred (Burnham and Anderson 2002: 168). Variable importance was then standardized to range from 0 to 1, which enabled us to compare equally across all of the variables.

To create a population-level estimate of resource selection, we used the individual estimates of selection coefficients with the following procedures. Adapting Biggerstaff and Tweedie (1997),  $B_i$  is the  $i = 1$  to  $K$  estimated selection

coefficient across  $K$  individuals. We assume a random effects model of the observed  $B_i$ s,

$$\begin{aligned} B_i &= \mu_i + \varepsilon_i, & \varepsilon_i &\sim N(0, \sigma_i^2) \\ \mu_i &= \mu + E_i, & E_i &\sim N(0, \tau^2) \end{aligned}$$

where  $\mu$  is the true underlying mean (the parameter of interest),  $\tau^2$  is the among individual variance, and  $\sigma_i^2$  is the error of the estimated selection coefficient for the  $i^{\text{th}}$  individual. We assume that the  $\sigma_i^2$  are known and substitute the estimated standard error of the selection coefficients for  $\sigma_i^2$ .

To estimate  $\mu$ , first set

$$w_i = \frac{1}{\sigma_i^2}; \quad S_1 = \sum w_i; \quad S_2 = \sum w_i^2$$

and then calculate an initial weighted mean across individuals,

$$\hat{\mu} = \frac{\sum w_i B_i}{S_1}.$$

Next, calculate the DerSimonian and Laird (1986) method-of-moments estimator of  $\tau^2$ ,

$$\hat{\tau}_{\text{DL}}^2 = \max \left\{ 0, \frac{\sum w_i (B_i - \hat{\mu})^2 - (K-1)}{S_1 - \frac{S_2}{S_1}} \right\}.$$

Using this estimate of the among individual variation, calculate new weights that take this variation into account,

$$w_i \left( \hat{\tau}_{\text{DL}}^2 \right) = \frac{1}{\sigma_i^2 + \hat{\tau}_{\text{DL}}^2}.$$

Using these new weights, calculate a final estimate of  $\mu$ ,

$$\hat{\mu} \left( \hat{\tau}_{\text{DL}}^2 \right) = \frac{\sum w_i \left( \hat{\tau}_{\text{DL}}^2 \right) B_i}{\sum w_i \left( \hat{\tau}_{\text{DL}}^2 \right)}$$

and the estimated variance of  $\hat{\mu}(\hat{\tau}_{\text{DL}}^2)$ ,

$$\text{vâr}\left[\hat{\mu}(\hat{\tau}_{\text{DL}}^2)\right] = \frac{1}{\left(\sum w_i(\hat{\tau}_{\text{DL}}^2)\right)^2} \times \sum \left[ w_i(\hat{\tau}_{\text{DL}}^2)^2 (\sigma_i^2 + \hat{\tau}_{\text{DL}}^2) \right]$$

The square root of this estimated variance is the standard error of  $\hat{\mu}(\hat{\tau}_{\text{DL}}^2)$ .

Thus, an approximate 95 percent confidence interval is:

$$\left\{ \hat{\mu}(\hat{\tau}_{\text{DL}}^2) - 1.96 \times \sqrt{\text{vâr}\left[\hat{\mu}(\hat{\tau}_{\text{DL}}^2)\right]}, \hat{\mu}(\hat{\tau}_{\text{DL}}^2) + 1.96 \times \sqrt{\text{vâr}\left[\hat{\mu}(\hat{\tau}_{\text{DL}}^2)\right]} \right\}$$



## APPENDIX E

### Synoptic Habitat Variables Description and Details

#### FOREST

Our study area consisted of seventeen major vegetation types including Douglas-fir, lodgepole pine, mixed spruce-fir, and sage steppe that were classified by the Montana Gap Analysis Program (GAP) land cover project (Redmond et al. 1998). In addition to GAP data, we used the grizzly bear Cumulative Effects Model (CEM) to assist with classifying burned areas into forested or nonforest types for our analyses (Mattson and Despain 1985; Mattson and Knight 1989). Overall, 71 percent of our study area consisted of forested cover (burned and unburned) versus 29 percent that was classified as nonforested or open—grass and shrub. Predominant on the study area were mixed spruce-fir and Douglas-fir—covering 43 percent and 35 percent of the forested area, respectively. Sage-steppe covered 35 percent of the nonforested study area.

We defined the variable, forest, as the number of forested 30 meter cells within a 240 meter buffer. Thus forest ranged from a count of 0 to 64.

#### TOPOGRAPHIC ROUGHNESS

We mapped terrain ruggedness using the terrain ruggedness index (TRI) of Riley and colleagues (1999) and the vector ruggedness measure (VRM) of Sappington and co-workers (2007) and evaluated the fit of these models to our study area. Both methods failed to reflect the topographically complex terrain in our study area adequately. Based solely on changes in elevation, the TRI method overestimated ruggedness on slopes that were steep but not topographically complex. The VRM method gave most emphasis to ridge tops and narrow valley bottoms and less emphasis to topographically complex slopes. We required an index that would map terrain consistent with our study area, in which

rough terrain consisted primarily of steep slopes with many small undulations. We therefore developed an index that gave equal weight to changes in elevation and aspect within an analysis window. Topographic roughness was calculated as the summation of:

- (1) The sum of the absolute value of the difference in elevation from one center cell ( $30 \times 30$  m) to its surrounding eight neighbor cells ( $3 \times 3$  window). This value was then standardized to range between zero and one, with one being sheer vertical cliff and zero being completely horizontal.
- (2) The number of different aspect categories (binned into 10 degree categories) in a  $3 \times 3$  window (range of one to nine), standardized to range between zero and one.

The final grid ranged from zero to two, with two being the maximum topographical roughness possible and zero representing completely flat areas. Fifty-seven percent of the study area was moderately to strongly topographically rough terrain. Topographic roughness was highly correlated with slope. We used topographic roughness in favor of slope because our TRI outperformed slope in our kill site analysis in chapter 7.

#### DISTANCE TO ESCAPE

Distance to escape was defined as the closest of either forest or high roughness. High roughness (roughness  $>1.1$ ) was subjectively defined based on field evaluation of the topographic roughness layer.

#### EDGE DENSITY

Edge was defined as the hard boundary between forest and nonforest. Edge density was calculated in meters of edge per square meter of ground.

## ELEVATION

Elevation was taken from a 30 meter Digital Elevation Model (DEM) obtained from the National Elevation Dataset (<http://ned.usgs.gov/>, accessed July 1, 2005) and converted to the average elevation within the 240 meter buffer.

## ROAD DENSITY

Road density was calculated following Schwartz and colleagues (2010) using a thematic layer of motorized routes from the Cumulative Effects Model (CEM) database for the Greater Yellowstone Ecosystem (GYE) created by the Interagency Grizzly Bear Study Team (IGBST; Schwartz et al. 2010). Total motorized route density (TMRD) was based on all roads, including those that were open, restricted (administrative access only), and closed to all motorized vehicular access (Ruth et al. 2011). We attributed telemetry locations with seasonal total road density within a 54 by 54 pixel (roaded 30 m cells/mi<sup>2</sup>, Trdann54) moving window (Ruth et al. 2011). We used the estimated average length of road of 25.8 meters per cell as found by Schwartz and co-workers (2010) and converted lengths to kilometers of road/km<sup>2</sup> when discussing road densities.

## SNOW WATER EQUIVALENT

Maps measuring snow water equivalent (SWE) in cm were estimated using a snow model for Yellowstone National Park developed at the Natural Resource Ecology Lab (<http://www.nrel.colostate.edu/projects/yellowstone/>; <http://www.nrel.colostate.edu/projects/yellowstone/Readme.htm>, accessed February 23, 2005), which incorporated climatological and cover type variables (Coughenour 1994; Coughenour and Singer 1996b; Farnes 1996; Farnes et al. 1999; Wockner et al. 2002). Daily values were averaged across the study area, and a snow map was created for each two-week period. We felt this metric would most appropriately capture the physical constraints that impede movements and foraging by large carnivores and herbivores during winter because the sinking depth of an animal is a function of snow depth, snow density, and hardness, which in turn influence energetic costs and the ability to capture prey and escape from competitors (Parker et al. 1984; Sweeney and Sweeney 1984; Gower et al. 2009b). Although snow water equivalent values trended higher in the wolf restoration period, we found no significant difference when averaging SWE across the study during

early, mid-, and late winter for each year and comparing to averages for the during wolf restoration study (early winter: Mann-Whitney  $U = 48$ ,  $P = 0.17$ ; midwinter: Mann-Whitney  $U = 29$ ,  $P = 0.93$ ; late winter: Mann-Whitney  $U = 44$ ,  $P = 0.83$ ).

## ELK USE

We used the PW restoration elk resource selection function (RSF) developed by Mao and colleagues (2005) as an index of elk use for the PW study period. We used the Mao and co-workers (2005) post-wolf restoration elk RSF model that included wolf use as the elk use index for the post-wolf restoration study period. Variables common to all models were cover type, elevation, slope, and snow water equivalent (in winter). Elk locations used to develop the PW models were collected between 1985 and 1990 (Singer 1988; Vore 1990; Vales and Peek 1996) and between 2000 and 2002 for the post-wolf models (Mao 2003; Mao et al. 2005). RSF layers were created for every two-week period in winter to account for changing snow conditions and every two months in non-winter to account for wolf movements. One non-winter elk RSF was created for the PW period. Cougar locations were attributed with the RSF value for the matching date. The model provided a good representation of elk use during winter, but the summer elk RSF potentially underestimates summer elk use in the Black Canyon of the Yellowstone. No radio-collared elk frequented the Black Canyon during summer, and thus the elk RSF maps predict elk use for the area that reflect core cougar habitat and in which cougars during the post-wolf time period made elk kills in the Black Canyon during summer.

## WOLF USE

For each yearly season (e.g., non-winter 2001), 95% utilization distribution (UD) grids (30 × 30 m cell size) were generated from the locations (limited to 1 location/pack/day) of all radio-collared wolves using Hawth's Analysis Tools for ArcGIS® ([www.spatialecology.com/htools/](http://www.spatialecology.com/htools/), accessed August 15, 2005) with a least squares cross-validation as the smoothing option (Kaufman et al. 2007; Ruth et al. 2011). Radio collars were distributed among wolf packs in proportion to pack size, so that wolf radio-locations were representative of the distribution of the YNP wolf populations (Mao et al. 2005). In addition, regression analyses indicated that the number of radio-collared wolves per pack was a good indicator of

pack size over each year ( $F = 131.83$ ,  $P = 0.000$ ,  $R^2 = 0.78$ ); thus high UD values occurred in areas with more wolves and reflected spatial variability in wolf use across the landscape (Ruth et al. 2011). Each yearly seasonal UD was then scaled by the number of wolves present to capture variability in the wolf population across seasons and years. Cougar locations were attributed with the wolf use value for the matching date. The wolf use index is a unit-less measure of relative wolf use across the Greater Yellowstone Northern Range and, when standardized, ranged from zero to one, representing a summer wolf density range of 20 to 56 wolves per 1,000 km<sup>2</sup> (average of 39/1,000km<sup>2</sup>) and a wolf density range of 29 to 82 per 1,000 km<sup>2</sup> (average of 58/1,000km<sup>2</sup>) on the Northern Range in winter (Smith et al. 2005, 2006). Densities were estimated using a 95 percent contour for all summer/winter wolf locations. Then density = wolf population/area \* 1,000.

## FEMALE COUGAR USE

This was included as a covariate for a subset of adult males during the time when the greatest number of adult males and adult females were radio-collared in each study—pre-wolf and during wolf. For each yearly season (e.g., non-winter 2001), 95 percent utilization distribution (UD) grids (30 × 30 m cell size) were generated for all radio-collared female cou-

gars using Hawth's Analysis Tools for ArcGIS®, and bandwidth was determined by likelihood cross-validation using Animal Space Use (Horne and Garton 2006b, 2007). Grids were rescaled to range from zero to one and summed. Male cougar locations were attributed with the female cougar use value for the matching date.

## CORRELATED VARIABLES

Prior to model fitting, variables were tested to ensure independence of variables. We did not include predictor variables correlated at  $r^2 > 0.5$  in the same model. Thus the following correlated variables were not included in the same a priori model.

- *Elk and elevation in summer* ( $r^2 = 0.82$  for during wolf study phase,  $P = 0.000$ )
- *Elevation and SWE in winter* ( $r^2 = 0.58$  for PW and  $r^2 = 0.50$  for during wolf study phases,  $P = 0.000$ )
- *Forest and edge density in summer* ( $r^2 = -0.53$  for PW and  $r^2 = -0.61$  for during wolf study phases,  $P = 0.000$ )
- *Forest and distance to escape in both seasons* ( $r^2 = -0.58$  to  $-0.73$  for both phases,  $P = 0.000$ )
- *Slope and topographic roughness in both seasons* ( $r^2 = 0.73$  to  $0.79$  for both seasons and phases,  $P = 0.000$ ).

## APPENDIX F

### Odds Ratios and Probability Ratios

#### A. LOGISTIC REGRESSION ODDS RATIO

Logistic regression models the response probability as:

$$p = \frac{\exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots)}{1 + \exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots)}$$

(Hosmer and Lemshow 2000; Manly et al. 2002). Holding all independent variables constant but one reduces to:

$$p = \frac{\exp(\beta_1 X_1)}{1 + \exp(\beta_1 X_1)}.$$

A probability ratio can then be calculated for any two values of an independent variable ( $X_a$  and  $X_b$ ), e.g.:

$$PR = \frac{\exp(\beta_1 X_a) / 1 + \exp(\beta_1 X_a)}{\exp(\beta_1 X_b) / 1 + \exp(\beta_1 X_b)}.$$

#### B. SYNOPTIC MODEL PROBABILITY RATIO

Probability of being in area a:

$$\Pr[y_a] = f(y_a) = \frac{f_0(y_a) \times \exp[\beta_1 X_{1a} + \beta_2 X_{2a} + \dots]}{\int \{f_0(y_a) \times \exp[\beta_1 X_{1a} + \beta_2 X_{2a} + \dots]\} dy}.$$

Probability of being in area b:

$$\Pr[y_b] = f(y_b) = \frac{f_0(y_b) \times \exp[\beta_1 X_{1b} + \beta_2 X_{2b} + \dots]}{\int \{f_0(y_b) \times \exp[\beta_1 X_{1b} + \beta_2 X_{2b} + \dots]\} dy}.$$

Now, if we want to know how much more likely we are to be in  $a$  than  $b$ , we can calculate:

$$\frac{\Pr[y_a]}{\Pr[y_b]}$$

which is, by definition, a “probability ratio.”

We get lucky when we put that monstrosity of an equation in for each of these probabilities. First, the integrals and cancel out, so we are left with:

$$\frac{\Pr[y_a]}{\Pr[y_b]} = \frac{\exp[\beta_1 X_{1a} + \beta_2 X_{2a} + \dots]}{\exp[\beta_1 X_{1b} + \beta_2 X_{2b} + \dots]}.$$

Next, if we are only interested in the effect of one covariate (i.e.,  $X_i$ ), we can set all other  $X$ s to a constant value so they can be removed:

$$\frac{\Pr[y_a]}{\Pr[y_b]} = \frac{\exp[\beta_i X_{ia}]}{\exp[\beta_i X_{ib}]}.$$

Next, if  $X_i$  = highest standardized value = 1 and  $X_i$  = lowest standardized value = 0, then we end up with:

$$\frac{\Pr[y_a]}{\Pr[y_b]} = \exp[\beta_i]$$

which is interpreted as the probability ratio of being in the area with highest value (area  $a$ ) versus lowest (area  $b$ ): “How many times more/less likely to be in  $a$  than  $b$ ?”



## NOTES

### CHAPTER 3. QUANTIFYING HOW SPECIES COMPETE OR COEXIST

- [1] Linear regression of cementum age and tooth wear ( $r^2_{adj} = 0.79$ ,  $P < 0.000$ ,  $n = 115$ ). Using this simple linear regression, cementum age equivalents were calculated with:

$$\text{Cementum Age Equivalent (months)} = 14.88 + 0.857 (\text{tooth wear in months}).$$

### CHAPTER 5. PREY SELECTION BY COUGARS AND WOLVES

- [1] Proportions of large and small ungulate prey killed were consistent across cougar social classes during the PW study phase (Fisher's exact test,  $P = 0.877$ ) and DW restoration (Likelihood ratio test,  $G_{adj} = 0.974$ ,  $df = 2$ ,  $P = 0.614$ ).
- [2] Prior to wolf restoration, elk and mule deer represented 77 percent and 23 percent of cougar kills, respectively, and 87 percent and 13 percent of the total abundance of these two species, respectively, averaged across all study years (Likelihood ratio test:  $G_{adj} = 17.7$ ,  $df = 1$ ,  $P < 0.0001$ ). During wolf restoration, elk and mule deer represented 84 percent and 16 percent of cougar kills, respectively, and 83 percent and 17 percent of the total abundance of these two species, respectively, averaged across all study years (Likelihood ratio test:  $G_{adj} = 0.71$ ,  $df = 1$ ,  $P < 0.400$ ). During the same time frame and proportional abundances of elk and mule deer, the wolf kill sample consisted of 98 percent elk and 2 percent mule deer (Likelihood ratio test:  $G_{adj} = 360.6$ ,  $df = 1$ ,  $P < 0.0001$ ).
- [3] The proportion of sex-age classes of elk and mule deer differed from their abundance across the study area (Likelihood ratio tests,  $P < 0.0001$  for both PW and DW study phases).
- [4] The PW kill sample consisted of 67 percent calves and 33 percent cows and bulls compared to 53 percent calves and 47 percent cows and bulls in the cougar kill sample DW restoration (likelihood ratio test,  $G_{adj} = 10.1$ ,  $df = 1$ ,  $P = 0.001$ ).
- [5] Proportions of adult males and females in the kill sample were consistent across reproductive seasons (Fisher's exact test,  $P = 0.173$ ).
- [6] The proportion of elk killed by cougars in each sex-age class of elk did not differ between winter and summer (Likelihood ratio test,  $G_{adj} = 2.68$ ,  $df = 3$ ,  $P = 0.443$ ).
- [7] Old cows made up 15 percent of the winter wolf diet and 5 percent of the summer wolf diet. With old cows removed, the proportion of elk killed by wolves in each sex-age class of elk did not differ between winter and summer (Likelihood ratio test,  $G_{adj} = 1.78$ ,  $df = 2$ ,  $P = 0.411$ ).
- [8] We found annual differences in the proportion of calves and adults killed across all years, 1999–2005 (Likelihood ratio test,  $G_{adj} = 21.8$ ,  $df = 6$ ,  $P = 0.001$ ). After collapsing data into early wolf restoration (1998–2001) and wolves restored (2002–5) periods, the proportion of calves versus adults killed did not differ during early wolf restoration (Likelihood ratio test,  $G_{adj} = 2.07$ ,  $df = 2$ ,  $P = 0.355$ ), but it did differ during the wolf restoration years, with adult elk making up an equal to greater proportion of the kill sample in these later years (Likelihood ratio test,  $G_{adj} = 7.37$ ,  $df = 3$ ,  $P = 0.061$ ).
- [9] Cougars selected for calves during early wolf restoration and after wolves were colonized (Likelihood ratio tests, both  $P < 0.0001$ ). Wolves also selected for elk calves each year 1999 through 2005 (Likelihood ratio tests, all  $P < 0.0001$ ).
- [10] After removing calves, we found no difference in the proportion of cows and bulls killed by cougars relative to availability of cows and bulls during the restoration and colonization periods (Likelihood ratio tests, both  $P > 0.60$ ). Wolves killed bull elk more often than expected in all years (Likelihood ratio tests, all  $P < 0.047$ ) except for 2001 (Likelihood ratio test,  $P = 0.157$ ).
- [11] Cougars and wolves killed similar proportions of prime-age and old cows during early wolf restoration and wolf colonized periods (Likelihood ratio tests, both  $P > 0.273$ ). The proportions of calves and bulls killed by cougars and wolves differed in both time periods (Likelihood ratio tests, both  $P < 0.001$ ).

- [12] The proportion of calves and prime-age cows in the diet of cougars and of calves and bulls in the diet of wolves changed as our study transitioned from early wolf restoration to after wolves were colonized (Likelihood ratio tests, cougars:  $G_{adj} = 11.05$ ,  $df = 3$ ,  $P = 0.011$ ; wolves:  $G_{adj} = 19.66$ ,  $df = 3$ ,  $P = 0.0002$ ).
- [13] Cougars killed 11 cows and wolves killed 67 cows in poor condition, compared to an expected value of 12.72 (Goodness of fit test,  $G_{adj} = 218.05$ ,  $P < 0.0001$ ).
- [14] Mean age of 17.6 (95% CI = 16.9–18.3) for old cows killed by cougars ( $n = 24$ ) was similar to the mean age of 17.2 (95% CI = 16.9–17.5) for old cows killed by wolves ( $n = 136$ ).
- [15] No difference in femur marrow fat of elk killed by cougars and wolves ( $F_{1,609} = 0.000$ ,  $P = 0.990$ ) or in interaction between predator and sex-age class of prey ( $F_{3,609} = 1.31$ ,  $P = 0.270$ ). After removing bulls, there still was no difference between predators or in interaction between predator ( $F_{1,466} = 1.55$ ,  $P = 0.213$ ) and sex-age class of prey ( $F_{3,466} = 0.11$ ,  $P = 0.900$ ).
- [16] Comparison of ages between adult elk with injuries, arthritis, or joint abnormalities ( $n = 13$ , median age = 11.0) and those with parasites ( $n = 11$ , median age = 9.0) (Mann-Whitney  $U = 165.0$ ,  $P = 0.908$ ). Comparison of femur marrow fat values between adult elk with injuries, arthritis, or joint abnormalities (median FMF = 49.8) and those with parasites (median FMF = 50.7) (Mann-Whitney  $U = 148.0$ ,  $P = 0.829$ ).
- [17] Comparison of femur marrow fat values between elk calves with injuries ( $n = 5$ , median FMF = 30.3) and those with parasites ( $n = 6$ , median FMF = 24.9) (Mann-Whitney  $U = 33.0$ ,  $P = 0.648$ ).
- [18] Although we explored exponential and quadratic models, the best fit to the data was a linear relationship (Linear regression,  $R = 0.51$ ,  $F = 16.5$ ,  $P = 0.001$ ).
- [19] The proportionality constant (95% CI) was 0.13 (0.05, 0.22) for the PW period and 0.12 (0.08, 0.15) for the DW study. Values of  $b$  averaged 2.37 (1.10, 3.47) across 16 PW and DW years.
- [20] Two points, corresponding to 1998 and 2005, appeared to have considerable influence on the curvilinear relationship. Once we removed these two points, the relationship was linear and values of  $b$  averaged 1.78 (1.06, 2.84) across 14 PW and DW years.
- [21] Variables that had correlation coefficients greater than 0.5 and that were not included in the same model were: snow water equivalent and elk use, distance to high roughness and roughness, distance to high roughness and distance to escape, distance to escape and openness.
- [22] At the kill site, odds were 922 times (95% CI = 218, 3,899) greater that a cougar kill occurred in rough terrain compared to wolf kills.
- [23] We tested for a difference in the distribution of cougar- and wolf-killed elk by first estimating the center—the average  $x$  and  $y$  location—of all cougar kills and also all wolf kills (Wilmers et al. 2003b). We then calculated the distance of each cougar kill to this central location for cougar kills and the distance of each wolf kill to the central location of the wolf kills. A Mann-Whitney test was then used to test for a difference in distribution between the two sets of distances. Test for difference in spatial distribution of cougar ( $n = 159$ , median = 8.2 km) and wolf kills ( $n = 447$ , median = 10.7 km) during early wolf restoration, 1998–2001 (Mann-Whitney  $U = 139.5$ ,  $P = 0.045$  adjusted for ties). Test for difference in spatial distribution of cougar ( $n = 127$ , median = 7.6 km) and wolf kills ( $n = 375$ , median = 11.5) during late wolf restoration, 2002–6 (Mann-Whitney  $U = 101.5$ ,  $P = 0.000$  adjusted for ties).
- [24] The receiver operating characteristics area under the curve (ROC AUC) for the top models in winter ranged from 0.51 to 0.54, indicating poor model fit for the variables included.
- [25] Test for differences of whether large prey and small prey kills occurred at different elevations ( $t_{424} = -3.08$ ,  $P = 0.002$ ) or on different slopes ( $t_{424} = -3.08$ ,  $P = 0.002$ ), or whether they differed in distance to escape cover ( $t_{226} = 3.31$ ,  $P = 0.001$ ).
- [26] Large prey were marginally positively associated with open areas ( $\chi^2 = 2.81$ ,  $P = 0.094$ ).
- [27] Large prey were positively associated with not being moved by cougars ( $\chi^2 = 17.30$ ,  $P = 0.000$ ).

## CHAPTER 6. RATES OF PREDATION

- [1] Tests for differences in kill rate, as days/kill, of cougars (social classes combined) prior to and during wolf restoration (Mann-Whitney  $U = 2612.5$ ,  $P = 0.262$ ). Mann-Whitney tests for differences in kill rate, as kills/day, of cougars prior to and during wolf restoration for adult males (Mann-Whitney  $U = 307.0$ ,  $P = 0.720$ ), adult females (Mann-Whitney  $U = 196.0$ ,  $P = 0.383$ ), and maternal females (Mann-Whitney  $U = 649.0$ ,  $P = 0.140$ ).
- [2] Relationship between kills/day/cougar and kilograms of prey/cougar for large prey (linear regression  $R^2 = 0.83$ ,  $F = 200.4$ ,  $P < 0.0001$ ) and small prey (polynomial regression  $R^2 = 0.69$ ,  $F = 176.6$ ,  $P < 0.0001$ ) differed.
- [3] Adult male, adult female, and maternal female PW cougars killed prey (days/kill) at different rates (Kruskal-Wallis tests:  $H = 5.21$ ,  $df = 2$ ,  $P = 0.074$ ). Adult male, adult female, and maternal female DW cougars killed prey (days/kill) at different rates (Kruskal-Wallis tests:  $H = 19.09$ ,  $df = 2$ ,  $P = 0.000$ ). We first looked within social classes and determined that individual cougars killed prey at very similar rates in both study phases. Thus no one individual had a strong influence on the kill rates within a social group. Kruskal-Wallis tests for differences in individual kill rates (kills/day) within social classes for PW cougars: adult females:  $H = 1.51$ ,  $P = 0.680$ ; adult males  $H = 1.77$ ,  $P = 0.412$ ; maternal females  $H = 4.54$ ,  $P = 0.209$ . Kruskal-Wallis tests for differences in individual kill rates (kills/day) within social classes for DW cougars: adult

- females:  $H = 7.52$ ,  $P = 0.275$ ; adult males  $H = 2.44$ ,  $P = 0.486$ ; maternal females  $H = 6.66$ ,  $P = 0.150$ .
- [4] Test for differences in kill rates, as log kg of ungulate/day, among cougar social classes (ANOVA, PW cougars  $F = 2.64$ ,  $P = 0.085$ ; DW cougars  $F = 1.34$ ,  $P = 0.267$ ). As with kills per day, individual cougars killed at a rate consisting of kilograms of prey per day similar to others in their social class, such that no one individual had an overriding influence on rate of kill. Kruskal-Wallis tests for differences in individual kill rates (kg of prey per day) within social classes for PW cougars: adult females  $H = 2.72$ ,  $P = 0.437$ ; adult males  $H = 0.08$ ,  $P = 0.961$ ; maternal females  $H = 6.30$ ,  $P = 0.198$ . Kruskal-Wallis tests for differences in individual kill rates (kg of prey per day) within social classes for DW cougars: adult females  $H = 7.05$ ,  $P = 0.217$ ; adult males  $H = 3.80$ ,  $P = 0.284$ ; maternal females  $H = 6.39$ ,  $P = 0.172$ .
- [5] Prior to wolves, adult females killed prey less frequently than did maternal females and adult males (Mann-Whitney tests,  $P < 0.066$ ), while maternal females and adult males killed at similar rates (Mann-Whitney test,  $P = 0.950$ ). During wolf restoration, maternal female cougars killed prey more frequently than did solitary females and adult males (Mann-Whitney tests,  $P < 0.001$ ), while solitary females and adult males killed at similar rates (Mann-Whitney tests,  $P = 0.182$ ).
- [6] Mann-Whitney tests for differences in kill rate, as log kg of ungulate/day, of cougars prior to and during wolf restoration for adult males ( $W = 302$ ,  $P = 0.779$ ), adult females ( $W = 118.5$ ,  $P = 0.133$ ), and maternal females ( $W = 500.5$ ,  $P = 0.965$ ).
- [7] We checked for statistical independence of kills to determine if our use of kill interval violated the assumption of independence prior to running multiple regression analyses. We found no correlation between a kill interval and the preceding kill interval when measured as days/kill ( $n = 90$ ,  $r^2 = 0.188$ ,  $P = 0.076$ ) or kg of biomass/day/kg of cougar ( $n = 84$ ,  $r^2 = 0.188$ ,  $P = 0.090$ ), indicating independence of kill observations.
- [8] Pre-wolf cougars spent less time (average = 2.5 days, median = 2.0) on a kill than did cougars during wolf restoration (average = 2.9, median = 3.0; Mann-Whitney  $U = 3245.0$ ,  $P = 0.034$ ).
- [9] Cats spent fewer days between kills during wolf presence (average = 4.1, median = 3.0) than prior to wolf presence (average = 5.6, median = 5.0; Mann-Whitney  $U = 2327.0$ ,  $P = 0.044$ ).
- [10] After removing displacements, cougars during wolf restoration still spent a median of 2 days less search-hunting time between kills than did their PW counterparts, and we could not reject our prediction that they should spend longer moving between kills (Mann-Whitney  $U = 2197.5$ ,  $P = 0.209$ ).
- [11] Adult male density carried 0.50 of the weight across models. Much of the 95 percent confidence interval around the  $\beta$  estimate was negative but still overlapped zero (see table 6.4); thus the effect on kill rate was not entirely clear.
- [12] Prior to wolves, males spent a median 1 day at a kill, which was less time at kills than solitary (Mann-Whitney  $U = 137.0$ ,  $P = 0.233$ ) and maternal females, but the difference was only significant compared to maternal females (Mann-Whitney  $U = 207.5$ ,  $P = 0.077$ ). Males spent a similar number of days moving between kills as did females supporting offspring (Mann-Whitney  $U = 263.5$ ,  $P = 0.531$ ) and a median of 3 days less between kills than solitary females (Mann-Whitney  $U = 149.5$ ,  $P = 0.068$ ).
- [13] Adult males traveled between kills for a median 1.5 days longer than maternal females (Mann-Whitney  $U = 1145.5$ ,  $P = 0.006$ ).
- [14] Adult males during wolf presence fed at kills longer than adult males prior to wolves (Mann-Whitney  $U = 247.0$ ,  $P = 0.047$ ), but they spent similar time moving between kills (Mann-Whitney  $U = 308.5$ ,  $P = 0.929$ ).
- [15] No difference in mean weight of prey killed by adult male, solitary female, or maternal female cougars prior to and during wolf restoration (ANOVA of log of prey weight by social class:  $F_{5,145} = 1.53$ ,  $P = 0.186$ ). No difference in proportion of large and small prey killed by PW adult females ( $n = 10$ ), PW maternal females ( $n = 14$ ), or PW adult males ( $n = 14$ ) (Fisher's exact test,  $P = 0.877$ ). No difference in proportion of large and small prey killed by DW adult females ( $n = 27$ ), DW maternal females ( $n = 58$ ), or DW adult males ( $n = 22$ ) during the PW study (Fisher's exact test,  $P = 0.608$ ). And no difference between study phases for any of the social classes (Fisher's exact test,  $P = 0.337$ ).
- [16] During wolf restoration, males spent a similar number of days feeding at kills as did solitary (Mann-Whitney  $U = 752.0$ ,  $P = 0.118$ ) and maternal females (Mann-Whitney  $U = 956.5$ ,  $P = 0.472$ ).
- [17] Solitary females spent longer between kills than did males and maternal females prior to wolves (Mann-Whitney tests, both  $P < 0.068$ ).
- [18] Solitary females spent longer between kills than did maternal females during wolf presence (Mann-Whitney  $U = 1495.0$ ,  $P = 0.001$ ).
- [19] Differences in days on a kill by social class during wolf restoration (Kruskal-Wallis test:  $H = 6.31$ ,  $df = 2$ ,  $P = 0.043$ , Mann-Whitney test to determine differences in social classes: adult female and maternal female cougars, Mann-Whitney  $U = 1414.5$ ,  $P = 0.017$ ).
- [20] Prior to wolf restoration, solitary females spent marginally longer moving between kills (Mann-Whitney  $U = 211.5$ ,  $P = 0.100$ ) and spent 2 days less feeding on kills than did DW solitary females, although the difference was not significant (Mann-Whitney  $U = 136.5$ ,  $P = 0.281$ ).
- [21] Test for differences in days maternal females spent at a kill prior to and during wolf restoration (median = 2.0 days

- in both study periods; Mann-Whitney  $U = 2105.0$ ,  $P = 0.870$ ).
- [22] Test for differences in days between kills by social class during wolf restoration (Kruskal-Wallis test:  $H = 13.89$ ,  $df = 2$ ,  $P = 0.001$ , Mann-Whitney test to determine differences in social classes: adult female and maternal female cougars, Mann-Whitney  $U = 1495.0$ ,  $P = 0.002$ ; adult male and maternal female cougars, Mann-Whitney  $U = 1145.5$ ,  $P = 0.006$ ).
- [23] Comparisons differed depending on how kill rate was measured: kg of prey/day, kg of prey/day/cougar, or kg of prey/day/kg of cougar. ANOVA for log kg of prey/day:  $F_3 = 2.10$ ,  $P = 0.103$ . ANOVA for log kg of prey/day/cougar:  $F_3 = 4.08$ ,  $P = 0.003$  significant differences from Tukey's pairwise comparison being a higher kill rate in PW winter compared to PW summer and PW winter to during wolf summer (a comparison not of interest). ANOVA for log kg of prey/day/kg of cougar:  $F_3 = 4.03$ ,  $P = 0.009$  with only significant difference from Tukey's pairwise comparison being PW winter to during wolf summer (a comparison not of interest).
- [24] Prior to wolves, large prey made up 7 percent and 21 percent of summer and winter kills, respectively, resulting in a greater winter kill rate (kg/day and kg/day/kg of cougar) of cougars (Likelihood ratio test,  $G_{adj} = 8.66$ ,  $df = 1$ ,  $P = 0.003$ ). During wolf restoration, the proportion of large prey was much more equitable between summer (32%) and winter (40%), resulting in little difference in cougar kill rates during the two seasons (Likelihood ratio test,  $G_{adj} = 1.53$ ,  $df = 1$ ,  $P = 0.216$ ).
- [25] Weak correlation between inter-kill interval and prey size during wolf restoration ( $R^2 = 0.53$ ,  $P = 0.074$ ).
- [26] Movement between kills was more strongly correlated with prey size ( $R^2 = 0.39$ ,  $P = 0.001$ ) than with handling time ( $R^2 = 0.26$ ,  $P = 0.024$ ).
- [27] Kill rate estimates produced by the ratio and inter-kill interval methods for the PW and during wolf study phases did not differ for kills/day/cougar (Kruskal-Wallis test:  $H = 5.83$ ,  $df = 3$ ,  $P = 0.120$ ), kg/day/cougar (Kruskal-Wallis test:  $H = 0.98$ ,  $df = 3$ ,  $P = 0.806$ ), or kg/day/kg of cougar (Kruskal-Wallis test:  $H = 0.77$ ,  $df = 3$ ,  $P = 0.856$ ).
- [28] Test for difference in days per kill by cougars, subadults included, and wolves (Two sample t-test,  $t_{69} = 9.70$ ,  $P = 0.000$  using log transformed kill rates to achieve normality).
- [29] Test for difference in kg/day kill rate by cougars, subadults included, and wolves (Two sample t-test,  $t_{49} = -11.93$ ,  $P = 0.000$  using log transformed kill rates to achieve normality).
- [30] Kill rate in kg/day/cougar was greater than kg/day/wolf (Two sample t-test,  $t_{32} = 3.30$ ,  $P = 0.002$  using log transformed kill rates to achieve normality).
- [31] Cougars also killed at a higher rate per biomass of cougars (kg/day/kg of cougar) compared to the wolf kill rate of kg/day/kg of wolves (Two sample t-test,  $t_{34} = 2.91$ ,  $P = 0.006$  using log transformed kill rates to achieve normality).
- [32] Our estimates for cougars and wolves and those of Becker and colleagues (2009b) reflect maximum intake because we did not account for incomplete consumption of inedible rumen or bone or for biomass lost to scavengers and competitors.
- [33] Prior to wolves: mean rate (SD) of 3.7 (2.3) days per kill for 65 elk kills and mean rate of 2.8 (2.0) days per kill for 28 mule deer kills. During wolf restoration, excluding displacements: mean rate (SD) of 8.3 (4.4) days per kill for 58 elk and mean rate of 6.7 (3.2) days per kill for 16 mule deer, pronghorn, and bighorn sheep kills.
- [34] A 45 kilogram Yellowstone female cougar as related to the average 88 kg elk calf, 250 kg adult elk, and 50 to 65 kg mule deer, pronghorn, or bighorn sheep that were killed by cougars during our study.

## CHAPTER 7. DIRECT INTERACTIONS AT KILLS

- [1] Wolves visited 23 percent (82 of 358) of cougar kills and displaced the cougar from 7.5 percent (27 of 358) of kills. Bears visited 50 percent (95 of 190) of cougar-killed ungulates in non-winter months when bears were active and displaced the cougar from 22 percent ( $n = 42$ ) of those kills. Test for difference between proportion of detections and displacements by wolves and bears (Detections:  $G_{adj} = 40.7$ ,  $df = 1$ ,  $P < 0.0001$ ; Displacements:  $G_{adj} = 22.5$ ,  $df = 1$ ,  $P < 0.0001$ ).
- [2] Cougars were displaced from 29 percent of kills in non-winter and 16 percent of kills in winter (Fisher's exact test,  $P = 0.007$ ; 95% CI for odds ratio = 1.2 to 3.8).
- [3] Six of 27 models had substantial support (Burnham and Anderson 2002) and accounted for 72 percent of the AICc weights of all candidate models (table 7.6). Because the 95 percent confidence intervals for beta estimates of the variables in the best model were bounded well away from zero, they were important factors for explaining displacement occurrence. The area under the ROC curve of 0.82 indicated that this model had very useful application for correctly predicting wolf displacement.
- [4] Two of 27 candidate models had  $\Delta AICc < 2$  and accounted for 58 percent of the AICc weights of all candidate models (table 7.4). This model had an ROC AUC of 0.80, indicating that it had very useful application for predicting bear displacement.
- [5] Large prey ( $n = 104$ ) killed by cougars tended to be on lower slopes (Mann-Whitney  $U = 91176.5$ ,  $P = 0.000$ ) and occurred in areas of greater wolf use than did small prey kills ( $n = 199$ ; test on variable wolf days, Mann-Whitney  $U = 27157$ ,  $P = 0.000$ ).
- [6] The additional variables of winter, elevation, and forest had small beta estimates (table 7.6), for which 95 percent confidence intervals included zero. Kills in forested areas comprised 84 percent of the sample and 74 percent of displacements by wolves, whereas winter kills comprised 63 per-



cent of the sample and 68 percent of displacements. Given these data, we were uncertain of the degree to which these variables were influencing wolf displacement occurrence.

- [7] The 95 percent confidence intervals around beta estimates for slope bounded zero, indicating that slope had a weaker influence than prey size, spring, and overall availability of carcasses.
- [8] Cougar predation rate, measured in kg of prey biomass per day, was higher when displacement occurred (95% CI for difference = 10.59 to 25.52 greater with displacement, Kruskal-Wallis test:  $H = 21.12$ ,  $P = 0.000$ ,  $n = 32$  wolf and bear displacement,  $n = 72$  no displacement). There was a greater difference when cougars were displaced from large kills (95% CI for difference = 11.83 to 40.75 greater with displacement, Mann-Whitney  $U = 375.0$ ,  $P = 0.001$ ,  $n = 34$  total large kills), than when they were displaced from small prey kills (95% CI for difference = 4.05 to 15.84 greater with displacement, Mann-Whitney  $U = 1240.5$ ,  $P = 0.001$ ,  $n = 88$  total small kills).
- [9] Cougars spent about 2 days longer (Mann-Whitney  $U = 247$ ,  $P = 0.003$ ) on large prey kills and 1 day longer (Mann-Whitney  $U = 766.5$ ,  $P = 0.014$ ) on small prey kills when other carnivores did not displace them.
- [10] There was no statistical difference in the rate at which adult male, solitary female, and maternal female cougars were displaced from kills ( $G_{adj} = 2.59$ ,  $df = 2$ ,  $P = 0.27$ ).

## CHAPTER 8. COMBINED INFLUENCES: COUGARS, WOLVES, AND HUMANS

- [1] Test for relationship between the total predation rate of cougars and numbers of elk (Linear regression provided the best fit,  $R^2_{adj} = 0.493$ ,  $F_{1,13} = 11.72$ ,  $P = 0.007$ ).
- [2] Test for relationship between the total predation rate of cougars and numbers of elk assuming elk numbers remained similar to PW levels (Linear regression,  $R^2_{adj} = 0.072$ ,  $F_{1,13} = 1.85$ ,  $P = 0.204$ ).
- [3] Test for relationship between the total predation rate of cougars and numbers of elk. Logistic regression yielded  $R^2 = 0.83$ , but too few data restricted fitting functions other than a linear model (Linear regression,  $R^2_{adj} = 0.743$ ,  $F_{2,13} = 32.82$ ,  $P = 0.0001$ ).
- [4] Test for relationship between the total predation rate of cougars and the ratio of cougars:1,000 elk (Linear regression,  $R^2_{adj} = 0.806$ ,  $F_{1,13} = 46.65$ ,  $P < 0.0001$ ).
- [5] Test for relationship between the total predation rate of wolves and the ratio of wolves:1,000 elk (Linear regression,  $R^2_{adj} = 0.97$ ,  $F_{1,8} = 173.61$ ,  $P < 0.0001$ ). A 3rd order polynomial yielded  $R^2 = 0.993$ , but too few data restricted fitting functions other than a linear model. Test for relationship between the total predation rate of cougars + wolves and the ratio of cougar + wolves:1,000 elk (Linear regression,  $R^2_{adj} = 0.86$ ,  $F_{1,13} = 68.26$ ,  $P < 0.0001$ ). A 3rd order polynomial yielded  $R^2 = 0.986$ , but too few data restricted fitting functions other than a linear model.
- [6] Test for relationship between the total predation rate of wolves and the ratio of wolves:1,000 elk (Linear regression,  $R^2_{adj} = 0.47$ ,  $F_{1,13} = 10.60$ ,  $P = 0.009$ ). A 4th order polynomial yielded  $R^2 = 0.859$ , but too few data restricted fitting functions other than a linear model.

## CHAPTER 10. SPATIAL RESPONSES OF COUGARS TO WOLF PRESENCE

- [1] Female home range and core areas did not differ between early and late wolf restoration periods (t-test on log of home range,  $t_{37} = -0.17$ ,  $P = 0.869$  and t-test on log of core area,  $t_{37} = 0.01$ ,  $P = 0.993$ ). We could not test between early and late wolf restoration periods for male ranges because we had too few estimates of ranges and core areas for males in the early wolf restoration period.
- [2] Female home ranges and core area sizes remained similar across PW and DW study years (ANOVA on log of home range and core areas, all  $0.249 < P < 0.788$ ). Annual home range and core area sizes of PW and DW adult females were not different (t-test on log of home range,  $t_{55} = 0.72$ ,  $P = 0.475$ ; t-test on log of core area,  $t_{52} = 0.53$ ,  $P = 0.599$ ). Combined annual and multi-year home ranges and core area sizes of PW and DW adult females also were not different (t-test on log of home range,  $t_{70} = 0.02$ ,  $P = 0.985$ ; t-test on log of core area,  $t_{72} = -0.13$ ,  $P = 0.894$ ).
- [3] One-sided test that annual home range sizes of adult females were smaller than adult male home ranges during the PW study (t-test on log of home range,  $t_{37} = -5.95$ ,  $P = 0.000$ ).
- [4] One-sided test that annual core areas of adult females were smaller than core areas of adult males during the PW study (t-test on log of home range,  $t_{38} = -6.84$ ,  $P = 0.000$ ).
- [5] One-sided tests that annual home range and core area sizes of adult females were smaller than adult male home ranges and core areas during the PW study (t-test on log of home range,  $t_{18} = -1.70$ ,  $P = 0.053$ ; t-test on log of core area,  $t_{19} = -2.08$ ,  $P = 0.026$ ).
- [6] Annual home range and core area sizes of PW adult males were significantly larger than home ranges and core areas of DW adult males (t-test on log of home range,  $t_{18} = 2.98$ ,  $P = 0.008$ ; t-test on log of core area,  $t_{19} = 3.02$ ,  $P = 0.007$ ).
- [7] Annual territories of wolves differed from home range sizes of adult female and PW adult male cougars (One-way ANOVA,  $F_4 = 11.5$ ,  $P = 0.000$ ). Fisher's pairwise comparisons indicated no differences in wolf territories and home ranges of DW adult male cougars. Annual core areas of wolves differed from those of adult female and male cougars prior to wolves (One-way ANOVA,  $F_4 = 13.6$ ,  $P = 0.000$ ).
- [8] Wolf home ranges and core areas were larger than home ranges and core areas of female cougars in both study phases

- (T-tests on log of home range size,  $t_{72} = -3.06$ ,  $P = 0.003$  for comparison with 95% fixed kernel home ranges of PW female cougars;  $t_{72} = -3.54$ ,  $P = 0.001$  for comparison with 95% fixed kernel home ranges of DW female cougars;  $t_{72} = -3.18$ ,  $P = 0.002$  for comparison with 50% fixed kernel core areas of PW female cougars;  $t_{47} = -3.07$ ,  $P = 0.004$  for comparison with 50% fixed kernel core areas of DW female cougars).
- [9] Home ranges and core areas of wolves were smaller than those of PW male cougars (T-tests on log of home range size,  $t_{33} = 4.50$ ,  $P = 0.000$  for comparison of 95% fixed kernel home ranges;  $t_{33} = 6.21$ ,  $P = 0.000$  for comparison of 50% fixed kernel core areas).
- [10] Home ranges and core areas of wolves did not differ from those of DW male cougars (T-tests on log of home range size,  $t_{51} = -0.66$ ,  $P = 0.515$  for comparison of 95% fixed kernel home ranges;  $t_{51} = 0.03$ ,  $P = 0.978$  for comparison of 50% fixed kernel core areas).
- [11] Calculations based on volume of intersection (VI) showed the same patterns as BA and so are not reported here.
- [12] Female fidelity in both study phases was lower when comparing home ranges 2 years apart to home ranges in consecutive years. Test for decline in fidelity between FI<sub>1</sub> and FI<sub>2</sub> for 95 percent fixed kernel home ranges for PW females (One-sided t-test  $t_{14} = 2.23$ ,  $P = 0.021$ ) and DW females (One-sided t-test  $t_{50} = 1.81$ ,  $P = 0.038$ ). Although a declining trend in fidelity was also observed in males, the difference between FI<sub>1</sub> and FI<sub>2</sub> was not significant. Test for decline in fidelity between FI<sub>1</sub> and FI<sub>2</sub> for PW males for 95 percent fixed kernel home ranges (One-sided Mann-Whitney  $U = 122.5$ ,  $P = 0.161$ ). Sample size for DW male cougars was too small for tests.
- [13] Test for difference in fidelity between home ranges and core areas for PW females (One-sided paired t-test on log of fidelity,  $t = 6.15$ ,  $P = 0.000$ ,  $n = 21$ ) and males (One-sided paired t-test on log of fidelity,  $t = 2.87$ ,  $P = 0.008$ ,  $n = 11$ ). Test for difference in fidelity between home ranges and core areas for females (One-sided t-test on log of fidelity,  $t = 9.28$ ,  $P = 0.000$ ,  $n = 33$ ) and males (One-sided t-test on log of fidelity,  $t_{17} = 1.81$ ,  $P = 0.044$ ,  $n = 8$ ) during wolf presence.
- [14] Test for difference in FI<sub>1</sub> fidelity to home ranges (Kolmogorov-Smirnov comparison,  $D = 0.434$ ,  $P = 0.001$ ) and core areas (Kolmogorov-Smirnov comparison,  $D = 0.378$ ,  $P = 0.008$ ) for PW ( $n = 32$ ) and DW periods ( $n = 41$ ). Because the KS-test reported that data were approximately lognormal, we took the log of all the data in a t-test, since the t-test is a more sensitive test. Two-sample t-test for differences in FI<sub>1</sub> fidelity for 95 percent home ranges ( $t_{71} = -2.72$ ,  $P = 0.008$ ) and 50 percent core areas ( $t_{71} = -3.69$ ,  $P = 0.000$ ). Two-sample t-test for differences in FI<sub>2</sub> fidelity for 95 percent home ranges ( $t_{39} = -2.72$ ,  $P = 0.010$ ) and 50 percent core areas ( $t_{39} = -2.00$ ,  $P = 0.052$ ). Because male and female cougars showed similar fidelity to home ranges and core areas within study phases and we had a low number of samples to examine male fidelity during wolf restoration, we pooled the sexes for comparisons between study periods. Test for difference in fidelity between males and females prior to wolves for home ranges (Kolmogorov-Smirnov comparison,  $D = 0.225$ ,  $P = 0.806$ ) and core areas (Kolmogorov-Smirnov comparison,  $D = 0.398$ ,  $P = 0.153$ ). Test for difference in fidelity between males and females during wolf restoration for home ranges (Mann-Whitney  $U = 117.0$ ,  $P = 0.10$ ) and core areas (Mann-Whitney  $U = 144.5$ ,  $P = 0.449$ ).
- [15] Test that male home ranges and core areas shifted more than those of females after three years' time, FI<sub>2</sub>. Test for difference in FI<sub>2</sub> home ranges (One-sided t-test on log of fidelity,  $t_{18} = -0.03$ ,  $P = 0.513$ ) and core areas (One-sided Mann-Whitney  $U = 88.5$ ,  $P = 0.379$ ).
- [16] We found no difference between early ( $n = 10$ ) and late ( $n = 14$ ) PW spatial overlap of home ranges for F-F pairs or early ( $n = 43$ ) and late ( $n = 30$ ) DW spatial overlap of home ranges for F-F pairs (Kruskal-Wallis test:  $H_3 = 1.02$ ,  $P = 0.796$ ). We found no difference between early ( $n = 19$ ) and late ( $n = 14$ ) PW spatial overlap of M-F pairs or early ( $n = 33$ ) and late ( $n = 33$ ) DW spatial overlap of M-F pairs (Kruskal-Wallis test:  $H_3 = 5.77$ ,  $P = 0.124$ ). We found no difference between early ( $n = 8$ ) and late ( $n = 12$ ) PW spatial overlap of core areas for F-F pairs (Mann-Whitney  $U = 64.0$ ,  $P = 0.132$ ) or early ( $n = 17$ ) and late ( $n = 13$ ) PW spatial overlap of M-F pairs (Mann-Whitney  $U = 248.0$ ,  $P = 0.530$ ). We found no difference between early ( $n = 21$ ) and late ( $n = 15$ ) DW spatial overlap of core areas for F-F pairs (Mann-Whitney  $U = 407.0$ ,  $P = 0.563$ ) or early ( $n = 28$ ) and late ( $n = 20$ ) DW spatial overlap of M-F pairs (Mann-Whitney  $U = 700.5$ ,  $P = 0.770$ ).
- [17] During the PW study, a larger percentage of a female's home range area was overlapped by males than by other females (Mann-Whitney  $U = 66.5$ ,  $P = 0.100$ ), but no difference was apparent when using the UD overlap index (Mann-Whitney  $U = 83.0$ ,  $P = 0.860$ ). During wolf restoration, a female's home range area was overlapped by males to a greater extent than by other females (UDOI, Mann-Whitney  $U = 100.0$ ,  $P = 0.088$ ), but no difference was found with percent overlap (Mann-Whitney  $U = 119.5$ ,  $P = 0.670$ ).
- [18] The inner contours, or core areas, of cougars prior to wolves overlapped with same-sex neighbors significantly less than their home ranges overlapped (females: one-sided Mann-Whitney  $U = 69.5$ ,  $P = 0.085$ ; males: one-sided Mann-Whitney  $U = 17.0$ ,  $P = 0.018$ ).
- [19] The inner contours, or core areas, of cougars during wolf restoration overlapped with same-sex neighbors equivalent to the amount their home ranges overlapped (females: one-sided Mann-Whitney  $U = 109.5$ ,  $P = 0.139$ ; males: one-sided Mann-Whitney  $U = 23.0$ ,  $P = 0.202$ ).

- [20] Female home ranges were overlapped (UDOI) to a greater extent by males during wolf restoration than prior to wolf presence (Mann-Whitney  $U = 58.5$ ,  $P = 0.007$ ), yet results with percent overlap did not support differences. Female core areas were overlapped to a greater extent (UDOI) by males during wolf restoration than prior to wolf presence (Mann-Whitney  $U = 58.0$ ,  $P = 0.006$ ), yet results with percent overlap did not support differences.
- [21] One-sided test that home range overlap of M-F pairs was greater than overlap of F-F pairs in the PW study period (Mann-Whitney  $U = 969.5$ ,  $P = 0.423$ ). One-sided test that overlap of core areas of M-F pairs was greater than overlap of F-F pairs in the PW study period (Mann-Whitney  $U = 797.5$ ,  $P = 0.263$ ).
- [22] Test for difference in home range overlap of F-F pairs between PW and DW study periods (Mann-Whitney  $U = 5235.0$ ,  $P = 0.511$ ).
- [23] Annual overlap between M-F pairs during wolf presence was greater than for M-F pairs prior to wolf presence. Test for difference in home range overlap of M-F pairs between PW and DW study periods (Mann-Whitney  $U = 2721.0$ ,  $P = 0.041$ ). One-sided test that home range overlap of M-F pairs was greater than overlap of F-F pairs during wolf restoration (Mann-Whitney  $U = 5235.0$ ,  $P = 0.005$ ). One-sided test that core area overlap of M-F pairs was greater than overlap of F-F pairs during the wolf restoration period (Mann-Whitney  $U = 2208.5$ ,  $P = 0.064$ ).
- [24] Test for relationship of home range size to the density of male and female cougars. Regression analyses for female cougars and male cougars to female density prior to wolf presence (all  $R^2_{\text{adj}}$  between 0.0% and 2.1%,  $P > 0.56$ ). Regression analyses for male cougars to male density ( $R^2_{\text{adj}} = 64.6\%$ ,  $P = 0.002$ ).
- [25] Test for relationship of home range size to the density of male and female cougars during wolf restoration. Regression of female home range size and female density ( $R^2_{\text{adj}} = 74.6\%$ ,  $P = 0.000$ ). Regression of female home range size and male density ( $R^2_{\text{adj}} = 49.0\%$ ,  $P = 0.000$ ). Regression of male home range size and female density ( $R^2_{\text{adj}} = 46.0\%$ ,  $P = 0.02$ ). Regression of male home range size and density of males ( $R^2_{\text{adj}} = 40.3\%$ ,  $P = 0.03$ ).
- [26] Using the average home range size of cougars, we found very little relationship for all models. For female and male home range size relationships with elk density during both studies all  $R^2_{\text{adj}} < 0.46$ ,  $P > 0.13$  except for PW males, where one data point had heavy influence and  $R^2_{\text{adj}} = 0.48$ ,  $P = 0.08$ . For male home range size relationships with cougar density during both studies  $R^2_{\text{adj}} < 0.35$ ,  $P > 0.13$ , and for female home range size relationships with cougar density  $R^2_{\text{adj}} = -0.17$ ,  $P = 0.22$  for PW females and  $R^2_{\text{adj}} = -0.21$ ,  $P = 0.73$  for DW females.
- [27] UDOI overlap of cougar and wolf summer home ranges (95% fixed kernel estimates) did not increase from early wolf restoration ( $n = 23$ , 1998–2001) and late wolf colonization ( $n = 23$ , 2001–5; one-sided t-test on log UDOI overlap,  $t_{70} = -0.78$ ,  $P = 0.218$ ).
- [28] UDOI overlap of wolves with cougar home ranges (95% fixed kernel estimates) was greater during winter than summer (one-sided t-test on log UDOI overlap early wolf restoration,  $t_{44} = -1.53$ ,  $P = 0.067$ ,  $n = 23$  summer and  $n = 23$  winter; one-sided t-test on log UDOI overlap wolf colonization,  $t_{100} = -3.98$ ,  $P = 0.000$ ,  $n = 49$  summer and  $n = 53$  winter). UDOI overlap of cougar and wolf home ranges increased between early wolf restoration ( $n = 23$ , 1998–2001) and late wolf colonization ( $n = 53$ , 2001–5; one-sided t-test on log UDOI overlap,  $t_{74} = -1.90$ ,  $P = 0.031$ ).
- [29] To make comparisons more analogous between the two species, we grouped movements into morning, midday, evening, and night periods. Test for differences of winter movement rates of female and male cougars and wolves during morning (0800–1000 hrs), midday (1100–1600 hrs), evening (1700–2100 hrs), and night (2200–0700 hrs) (ANOVA  $F_{11} = 68.62$ ,  $P = 0.000$ ). Fisher's pairwise comparisons indicated differences in movement rates for female and male cougars compared to wolves during all time periods. Test for differences of summer movement rates of female and male cougars and wolves during morning (0800–1000 hrs), midday (1100–1800 hrs), evening (1900–2100 hrs), and night (2200–0700 hrs) (ANOVA  $F_{11} = 116.2$ ,  $P = 0.000$ ). Fisher's pairwise comparisons indicated differences in movement rates for female and male cougars compared to wolves with the exception of male cougars moving at similar rates as wolves during midday and evening.
- [30] Test for difference in movement rate of female cougars when they were in their core area, in the core area of wolves, or in neither core area. We only found significant differences for winter night (ANOVA,  $F_3 = 26.7$ ,  $P = 0.000$ ) and summer night (ANOVA,  $F_3 = 4.0$ ,  $P = 0.009$ ). In both cases, Tukey pairwise comparisons showed differences for movement rates when females were in cougar cores, wolf cores, and neither.
- [31] Test for difference in movement rate of male cougars when they were in their core area, in the core area of wolves, or in neither core area. We only found significant differences for winter day (ANOVA,  $F_3 = 2.5$ ,  $P = 0.060$ ). Tukey pairwise comparisons showed differences for movement rates when males were in wolf cores and outside either cougar or wolf core areas.
- [32] Mann-Whitney  $U$  tests for differences between observed simultaneous distances and expected distances during summer were random (range in probability:  $P = 0.12$  to  $0.70$ ). Two cats showed attraction to wolves and one cat showed avoidance (all  $P = 0.000$ ).

- [33] Mann-Whitney  $U$  tests for differences between observed simultaneous distances and expected distances during summer were random (range in probability:  $P = 0.13$  to  $0.99$ ). Seven cats showed attraction to wolves (all  $P < 0.04$ ).

## CHAPTER 11. PATTERNS OF RESOURCE USE PRIOR TO AND DURING WOLF RESTORATION

- [1] Maternal females, solitary females, and adult male cougars all moved greater distances at night than during the day after we pooled locations into day (morning and afternoon locations representing primarily bed sites and less movement) and night (evening and night locations when cougars were primarily hunting and traveling). Mann-Whitney tests on distance moved between consecutive locations (3-hr interval) were all significant at  $P < 0.01$ . See statistics in chapter 10.
- [2] The amount of forest was correlated with edge density and distance to escape, and elevation was correlated with elk use and snow water equivalent (all  $P = 0.000$ ). Correlated terms were not included in the same additive models. In addition, we chose topographic roughness for use in our model set over slope because of the high correlation, greater than  $-0.72$ , of these two variables ( $P = 0.00$ ). See appendix D.
- [3] Similar landscape variables were included in top models and, with a few exceptions, the direction of beta coefficients did not change.
- [4] Although male cougars were less likely to use areas of increasing wolf use, the relationship became less clear as wolf use increased—95 percent confidence intervals bounded zero at values between  $0.14$  and  $0.36$  (the highest wolf use used by male cougars).
- [5] The effect of elk use on male cougars during wolf presence was inconclusive, in that the confidence intervals were very wide and bounded zero.
- [6] In all but two of the top models that included adult female use, the 95 percent confidence interval around the beta estimate of its influence on male space use bounded zero.
- [7] Betas in the top model sets for summer and winter and at the point and buffer bounded zero, and odds ratios were near zero to one.
- [8] There was no difference in the distributions of distance to escape cover during winter day ( $n = 2,017$ ) and night ( $n = 4,680$ ) and during summer day ( $n = 3,982$ ) and night ( $n = 3,732$ ). Two-sample Kolmogorov-Smirnov test for winter  $D = 0.013$  and summer  $D = 0.03$ ,  $P > 0.166$  for both tests.
- [9] We did not use elevation and snow water equivalent in the same model because they were correlated variables, but elk use and snow water equivalent were not correlated and thus were used in the same model (see appendix E).

## CHAPTER 14. COUGAR POPULATION STRUCTURE

- [1] Test for differences in proportion of adult females ( $Z$ -test =  $-0.52$ ,  $P = 0.601$ ) and adult males ( $Z$ -test =  $-0.26$ ,  $P = 0.798$ ) between PW and DW study phases. After combining study phases, a mean 44 percent to 57 percent (95% CI) of the study population was composed of adult cougars, and kittens and subadults made up 31–43 percent and 7–17 percent, respectively.
- [2] Ages of adult males were similar across all PW study years (Kruskal-Wallis test:  $H = 3.68$ ,  $df = 7$ ,  $P = 0.815$ ), as were those of adult females (Kruskal-Wallis test:  $H = 1.92$ ,  $df = 7$ ,  $P = 0.983$ ).
- [3] Ages of adult males and females were similar prior to wolf restoration ( $t$ -test on  $\ln$  age,  $t_{88} = 1.26$ ,  $P = 0.212$ ).
- [4] During wolf restoration, mean ages of adult males were similar across all study years (Kruskal-Wallis test:  $H = 7.30$ ,  $df = 5$ ,  $P = 0.199$ ), but mean ages of females increasingly grew older as the study progressed (Kruskal-Wallis test:  $H = 15.91$ ,  $df = 7$ ,  $P = 0.026$ ).
- [5] Adult females were older than adult males during wolf restoration ( $t$ -test on  $\ln$  age,  $t_{86} = 2.30$ ,  $P = 0.024$ ).
- [6] Mean ages of adult females ( $n = 59$ ) and adult males ( $n = 28$ ) prior to wolf restoration were younger than those of females ( $n = 67$ , Mann-Whitney  $U = 3001.5$ ,  $P = 0.000$ ) and males ( $n = 20$ , Mann-Whitney  $U = 3001.5$ ,  $P = 0.048$ ) during wolf restoration.
- [7] There was no difference between numbers of individuals monitored per year between study phases and sexes ( $\chi^2 = 0.133$ ,  $P = 0.754$ ).
- [8] There was no difference in median length of monitoring for female kittens between study phases (Mann-Whitney  $U = 645.5$ ,  $P = 0.286$ ). The median length of monitoring was less for male kittens in the PW than in the DW study (Mann-Whitney  $U = 626.0$ ,  $P = 0.029$ ).
- [9] Mean sex ratios of kittens did not differ from a hypothetical 1:1 sex ratio (Likelihood ratio test,  $G_{adj} = 0.494$ ,  $df = 1$ ,  $P > 0.482$ ). Male:female sex ratio of kittens  $\leq 8$  weeks old did not differ between PW ( $n = 36$  kittens in 14 litters) and DW ( $n = 36$  kittens in 13 litters) study phases (Likelihood ratio test,  $G_{adj} = 1.97$ ,  $df = 1$ ,  $P = 0.161$ ).
- [10] The sex ratio of subadult cougars did not differ from a hypothetical 1:1 sex ratio prior to or during wolf restoration (Likelihood ratio tests,  $G_{adj} < 1.45$ ,  $df = 1$ ,  $P > 0.228$ ).
- [11] The female-biased sex ratio of subadult cougars prior to wolves differed from the male-biased sex ratio of cougars during wolf restoration (Likelihood ratio tests,  $G_{adj} = 4.64$ ,  $df = 1$ ,  $P = 0.031$ ).
- [12] Mean sex ratios of adults did not differ between study phases or from a hypothetical 1:1 sex ratio (Likelihood ratio tests, all  $G_{adj} < 2.10$ ,  $df = 1$ ,  $P > 0.147$ ).



- [13] Adult sex ratios for March–April population estimates did not differ from 1:1 (Likelihood ratio tests, all  $G_{adj} < 2.19$ ,  $df = 1$ ,  $P > 0.14$ ) except for 1992–93 of the PW study (Likelihood ratio test,  $G_{adj} = 3.27$ ,  $df = 1$ ,  $P = 0.071$ ) and 1999–2000 (Likelihood ratio test,  $G_{adj} = 2.88$ ,  $df = 1$ ,  $P = 0.090$ ) and 2001–2 (Likelihood ratio test,  $G_{adj} = 3.90$ ,  $df = 1$ ,  $P = 0.048$ ) of the DW study.

## CHAPTER 15. REPRODUCTION AND SURVIVAL RATES OF COUGARS

- [1] Comparison of distribution of births to a uniform distribution across months (Kolmogorov-Smirnov test,  $D = 0.583$ ,  $P = 0.019$ ).
- [2] Litters were composed of 2 kittens ( $n = 6$  PW litters,  $n = 5$  DW litters), 3 kittens ( $n = 7$  PW litters,  $n = 5$  DW litters), and 4 kittens ( $n = 3$  PW litters,  $n = 3$  DW litters).
- [3] Test for difference in mean litter size of cougars prior to and during wolf restoration (t-test,  $t_{27} = -0.16$ ,  $P = 0.874$ ).
- [4] Kittens older than 9 weeks were marked at 10–52 weeks of age in the PW study and 9.5–54 weeks of age during wolf restoration. Test for difference in mean litter size for litters marked at greater than 9 weeks of age prior to and during wolf restoration (t-test,  $t_{27} = 1.99$ ,  $P = 0.058$ ).
- [5] Test for difference in proportion of 1, 2, 3, and 4 kittens per litter prior to and during wolf restoration (Likelihood ratio test,  $G_{adj} = 3.059$ ,  $df = 3$ ,  $P = 0.382$ ).
- [6] No difference in birth interval between PW ( $n = 15$  intervals) and DW ( $n = 17$  intervals) study periods for all litters, including those that survived to independence and those that did not (Mann-Whitney  $U = 207.5$ ,  $P = 0.136$ ).
- [7] Birth interval averaged 5 months longer in the wolf restoration study (Mann-Whitney  $U = 41.0$ ,  $P = 0.017$ ) and was  $12.7 \pm 2.1$  months ( $n = 8$  intervals) prior to wolves and  $21.5 \pm 7.5$  months ( $n = 6$  intervals) during Phase II.
- [8] Test for difference in maternity rates prior to and during wolf restoration (Z-test,  $Z = 2.332$ ,  $P = 0.020$ ). Maternity rate was higher during the PW study phase (maternity rate = 1.65; 95 percent confidence interval = 1.22–2.08) than during wolf presence (maternity rate = 1.08; 95 percent confidence interval = 0.75–1.41).
- [9] Test for difference in maternity rates for female offspring prior to and during wolf restoration (Z-test,  $Z = 1.67$ ,  $P = 0.094$ ). Test for difference in maternity rates of male offspring prior to and during wolf restoration (Z-test,  $Z = -0.79$ ,  $P = 0.431$ ).
- [10] Females >6 years old and females 2 to 6 years old produced at a similar frequency. Chi Square test = 2.01,  $df = 1$ ,  $P = 0.157$  (Biek et al. 2006d).
- [11] Causes of kitten mortality differed between PW and DW study phases when we examined finer categories of infanticide, dominant competitors, and natural deaths (orphaning/disease; Likelihood ratio test,  $G_{adj} = 12.77$ ,  $df = 2$ ,  $P = 0.002$ ).
- [12] The effect of a mother's age on kitten survival was not clear in models that included this covariate as 95 percent confidence intervals around the  $\beta$  estimates bounded zero.
- [13] Most kittens died during winter in both the PW (81% in winter) and DW study phases (65% in winter). Test for equality of time of death in winter ( $n = 30$ ) versus summer ( $n = 11$ ) (Likelihood ratio test,  $G_{adj} = 4.62$ ,  $P = 0.032$ ).

## CHAPTER 16. DISPERSAL AND POPULATION CHANGE

- [1] Although cougars spent time independent from their mothers before dispersing for slightly longer during wolf presence ( $n = 26$ , 95% CI = 16.5 to 35 days, median = 19 days) compared to PW restoration ( $n = 21$ , 95% CI = 11.8 to 20.1 days, median = 15 days), the difference was not significant (Mann-Whitney  $U = 472.5$ ,  $P = 0.507$ ).
- [2] The median home range diameter of female cougars was 23.8 km, and the median home range diameter of male cougars was 34.1 km.
- [3] Test for difference in age offspring became independent from their mothers prior to (median age = 12.8 months) and during wolf restoration (median age = 15.2 months; Mann-Whitney  $U = 471.0$ ,  $P = 0.000$ ).
- [4] Test for difference in age offspring emigrated from the study area prior to (median age = 12.8 months) and during wolf restoration (median age = 19.7 months; Mann-Whitney  $U = 471.0$ ,  $P = 0.000$ ).
- [5] Test for difference in proportions of subadults surviving to dispersal age and emigrating from the study area before and during wolf restoration (surviving to dispersal: Likelihood ratio test,  $G_{adj} = 1.02$ ,  $df = 1$ ,  $P = 0.312$ ; emigrating: Likelihood ratio test,  $G_{adj} = 0.157$ ,  $df = 1$ ,  $P = 0.692$ ).
- [6] About 1.6–2.0 females and 1.4–1.7 males emigrated per year prior to wolf restoration. Following the restoration of wolves, about 2.0–2.1 females and 1.7–2.3 males emigrated per year.
- [7] Test for difference in proportion of female and male subadults establishing prior to ( $n = 5$  females, 6 males) and during wolf restoration ( $n = 6$  females, 8 males; Likelihood ratio test:  $G_{adj} = 0.016$ ,  $df = 1$ ,  $P = 0.900$ ).
- [8] Test for difference in age at death of successful emigrant females ( $n = 8$ ) and males ( $n = 12$ ) combined across study phases (Mann-Whitney  $U = 107.0$ ,  $P = 0.083$ ).
- [9] Test for difference in age at death of successful emigrant females ( $n = 8$ ) and males surviving beyond 30 months of age ( $n = 4$ ) combined across study phases (Mann-Whitney  $U = 52.0$ ,  $P = 1.00$ ).
- [10] We used the top synoptic model set ( $\geq 90$  percent of model weights) for each individual cougar and averaged them to create one utilization distribution for each individual

(chapter 11). As in model development, snow water equivalent, wolf use, and elk use attributes were allowed to vary by 2-week intervals. Each 2-week interval was then averaged to create a static map for the time periods depicted by the maps.

- [11] Although our abundance and immigration rates were derived from a near-complete annual census with individuals back-calculated into the population, the minor sampling variance we expected could not be separated from process variance. The sampling variance included in our estimates should be greatest for the first 2 years of each study period as we began our efforts to determine the numbers of cougars. By not accounting for sampling variance, our 95 percent confidence interval estimates of population growth may be somewhat inflated compared to if we had been able to base estimates on process variance only (Mills 2007; see also Newby et al. 2013).
- [12] Sensitivity and elasticity were 0.17 for both kittens and sub-adults prior to wolf restoration and 0.12 for both kittens and subadults during wolf restoration.

## CHAPTER 17. SYNTHESIS: THE NICHES OF COUGARS AND WOLVES

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- [1] Using the Renkonen index (1938, in Krebs 1999), the diet of cougars and wolves overlapped by 82 percent across seasons in the period 1998–2005 (Renkonen index, Murphy and Ruth 2010). We also determined overlap in prey use between cougars and wolves using the Pianka (1973) measure of niche overlap and program EcoSim 12 (Entsminger 2013). After incorporating prey abundance, pairwise comparisons of diets during early and late wolf restoration showed high overlap of 0.96 and 0.9, respectively. One thousand Monte-Carlo simulations were run using the program EcoSim 12 (Entsminger 2013) to determine whether the observed overlap was greater or lower than random expectation. The mean overlap index across periods of 0.31 and greater than random expectation of  $0.24 \pm 0.003$  variance suggested both exploitation competition and resource partitioning between cougars and wolves.
- [2] Levins's (1968) niche breadth was 1.5 for cougars and 1.1 for wolves. We standardized niche breadth using Hurlbert's (1978) measure, resulting in a niche breadth for cougars (0.085) that was 7 times the niche breadth of wolves (0.012).

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